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BULLETIN OF THE TORREY BOTANICAL CLUB
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NOTES ON THE HYPHOMYCETOUS GENERA, SPEGAZZINIA SACC. AND ISTHMOSPORA STEVENS

SAMUEL C. DAMON[1]

During the course of an investigation into some of the genera producing dark-colored dictyospores, it became evident that within the genus *Spegazzinia* there had been included a number of species varying quite widely from the type. The present study was carried out to establish more precisely those species which should continue to be regarded as belonging to the genus and to give those which belong elsewhere or should be regarded as synonyms a more reasonable disposition based upon examination of type or authentic material whenever possible. The best known species, reported variously as *S. ornata* Sacc. or *S. tessarthra* (B. and C.) Sacc., is of rather common occurence on rotting plant (particularly monocotyledonous) substrates in tropical and subtropical regions and appears to be one of the agents responsible for deterioration of other cellulose-containing materials in these areas. *Isthmospora*, a small and poorly known genus, was studied concurrently when it was found that several species of *Spegazzinia* were identical with its type species, *I. spinosa*.

Spegazzinia was placed among the dark-spored, dictyosporous genera of the Tuberculariaceae by Saccardo (1880), who erected it for the single species *S. ornata*, based upon a collection on dead leaves of *Andropogon Gryllus* from Italy. Since that time, twelve other species have been added and are listed below in chronological order:

Spegazzinia ornata Saccardo, 1880.
" *effusa* Karsten, 1884.
" *ammophila* Rostrup, 1896.
" *tucumanensis* Spegazzini, 1896.
" *trichophila* Atkinson, 1897.
" *calyptrospora* von Höhnel, 1902.
" *meliolae* Zimmermann, 1902.
" *lobata* (B. and Br.) von Höhnel, 1903.
" *meliolicola* Hennings, 1904.
" *coffeae* Hennings, 1906.
" *brasiliensis* Spegazzini, 1919.
" *rubra* Dearness and House, 1923.
" *chandleri* Hansford, 1943.

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[THE BULLETIN for March–April, 1953 (80: 113–153) was issued March 18, 1953]

As in most hyphomycetes, the distinguishing features of *Spegazzinia ornata* lie in the morphology of its conidia and the arrangement of its conidiophores; and a brief consideration of these characteristics of this species will be useful in establishing the limits of the genus as well as of its type species. In this species the spores are of two types, one smooth-walled, the other echinulate, and both dark-colored with the four adjacent triangular cells arranged in the pattern of a four-leaf clover imparting a square or slightly rectangular shape to the spores. This striking arrangement (obscured in the echinulate, enlarged type) is most apparent in the smooth-walled spores (fig. 2, G,H,J). Both spore forms are present in most specimens and isolations, although a few have been studied in which only the smooth-walled type were seen; and in every case having both types, the echinulate are less abundant. In addition to these two types, which may be called the normal forms, there are also abnormal, variously-shaped dictyospores (van Overeem 1923), the size and shape of such spores differing widely from the normal and usually being smooth-walled although the spore illustrated in figure 2, G is an example of an abnormal form of an echinulate spore. It has also been observed that in many cases the type of spore which predominates determines the character of the sporodochium in which it is borne. When the smooth-walled spores are most numerous, the sporodochia are usually compact and closely appressed to the substratum (fig. 1, A); but when the echinulate type predominates as in figure 1, B, the sporodochium has a more scattered, loose appearance. This difference arises from the fact that smooth-walled spores are formed on short branches of the substratal hyphae whereas the echinulate spores arise at the apex of long, dark-colored, simple, smooth or slightly roughened conidiophores.

From the foregoing discussion it seems not unreasonable to include in *Spegazzinia* those species having four-celled spores which are either smooth-walled or echinulate and are borne as terminus spores on simple conidiophores arranged in sporodochia. Inspection of this characterization and of the discussion of other species which follows will reveal that *Spegazzinia* seems to be arbitrarily limited to the type species. This has been done purposely so as to prevent unnecessary changes in other established genera at a time when too little information is available regarding them. As constituted above, *Spegazzinia* may be separated from *Tetracoccosporium* on the lack of sporodochia in the latter and from *Isthmospora* on the morphology of its spores and for other reasons given below.

With this understanding of the genus it is possible to proceed to a consideration of the other species. As has been mentioned already, *S. ornata* was the only species described by Saccardo (1880) and is, therefore, the type species. An identical organism had been described earlier by Berkeley and Curtis (1869) as *Sporidesmium tessarthrum* from material collected

in Cuba by Wright, and was transferred to *Spegazzinia* as a distinct species by Saccardo (1886) with the comment that he was not satisfied with Cooke's statement pointing out the identity of *S. ornata* with *S. tessarthra* (Cooke & Harkness 1884). Examination of isotype specimens of *Sporidesmium*

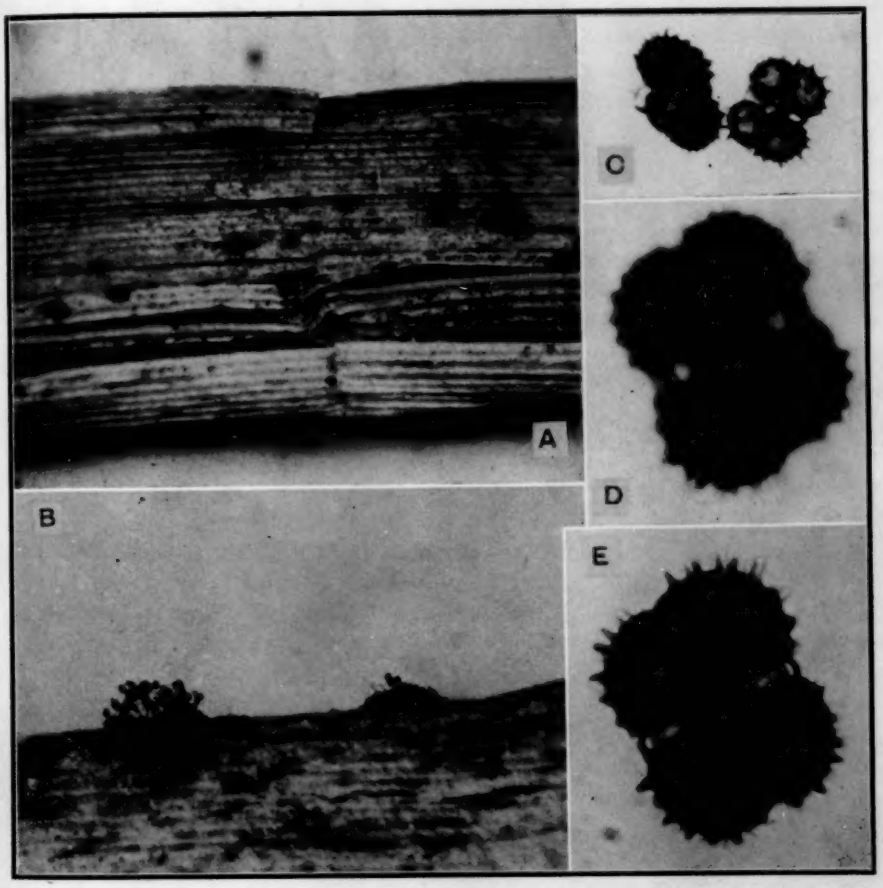

FIG. 1. A. Habit of *Spegazzinia ornata*, authentic. × 10. B. Side view of two sporodochia of *S. tessarthra* showing loose and compact arrangement of conidiophores and echinulate spores. × 10. C. Spores of *Spegazzinia trichophila* Atk., type. × 750. D. Enlarged view of spore of *S. trichophila* to show "isthmus" cells and upper pair of peripheral cells. E. Same spore as in D. but focused lower to show lower pair of peripheral cells × 1500.

tessarthrum B. and C. from the Curtis herbarium (fig. 2, H) indicates the correctness of Cooke's opinion and *S. ornata* is now considered to be a synonym of *S. tessarthra* (B. and C.) Sacc., the latter name being that by which the type species is known. In discussing this problem, Cooke considered this species under *Tetrachia quadrigemina* B. and C. with the fol-

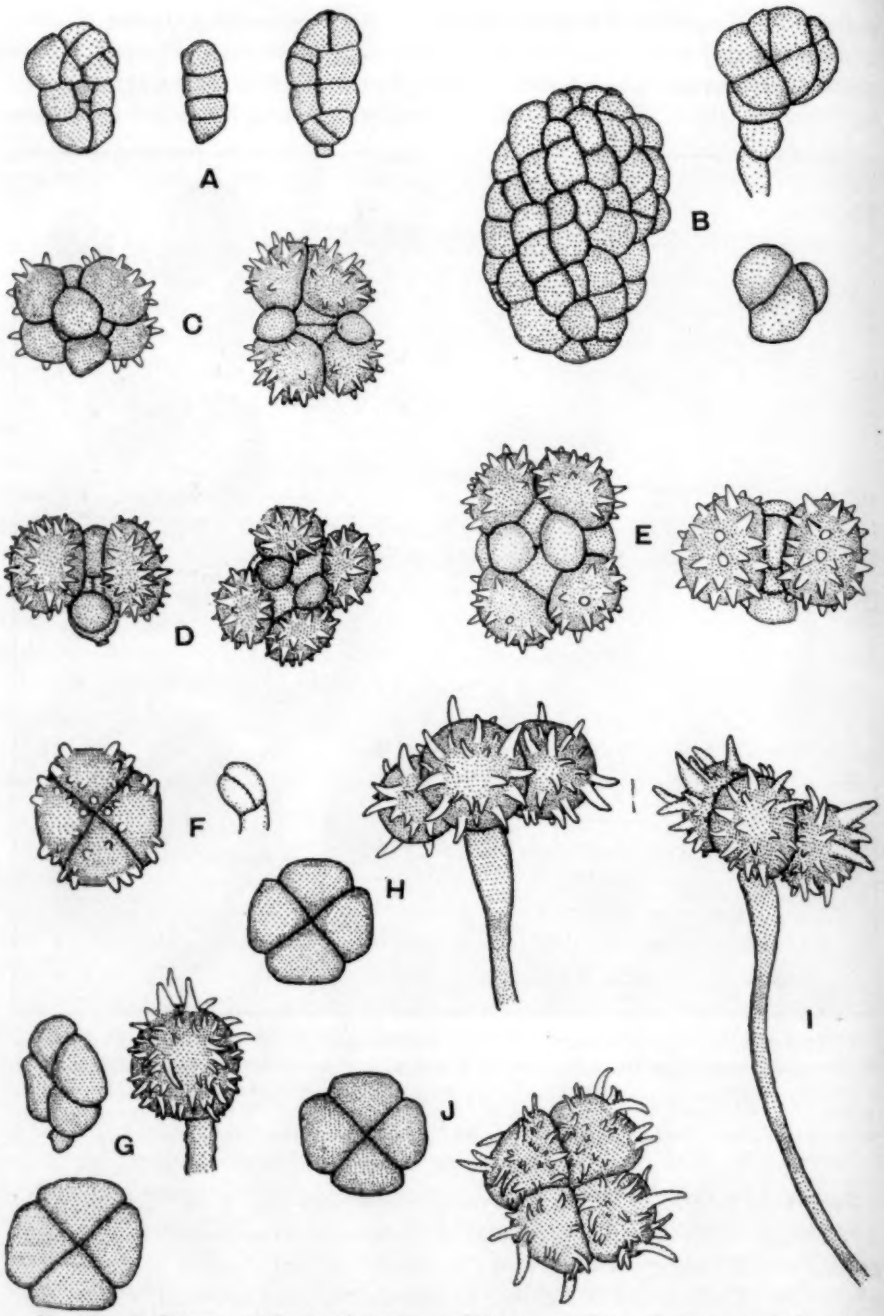

FIG. 2. A. Spores of *Spegazzinia ammophila*, type. × 750. B. Spores of *S. calyptrospora*, type. × 1500. C. Spores of *S. trichophila*, type. × 1500. D. Spores of *S.*

lowing description: "*Tetrachia quadrigemina* Berk. and Curt. This is the *Sporidesmium tessarthrum* B. and C. and the *Spegazzinia ornata* Sacc., found originally in Cuba, and Venezuela." The only record of this name, other than that given here, is as an herbarium name (in herb. Curt.). Saccardo (1918) discussed Cooke's description and decided that it was not valid publication of the generic name which was, therefore, a *nomen nudum*, but used the name *Tetrachia* himself for an organism which Sydow and Sydow (1921) say is identical with that discussed here as *Isthmospora trichophila*. It is also my own feeling that Cooke's mention of the name does not constitute valid publication and it may be rejected according to Article 41 of the International Rules of Botanical Nomenclature. Other species which must fall into the synonomy of this species are *Triposporium cristatum* Pat. (Patouillard & Gaillard 1888) and *Spegazzinia tucumanensis* Spegazzini (Spegazzini 1896). Examination of the type specimens as well as the descriptions of both show that neither differs in any way from *S. tessarthra*. It is also highly probable from its description that *Spegazzinia brasiliensis* Spegazzini (Spegazzini 1919) should be disposed here, but the type material of this species appears to be lost (personal communication, J. Lindquist).

Of the other species, *S. trichophila, S. meliolae, S. meliolicola* and *S. coffeae* must be considered together, and with them, *Isthmospora spinosa* Stevens (Stevens 1918). All of these have been based upon an organism found growing in more or less close association with species of *Meliola* on leaves of tropical and subtropical plants. In most discussions a parasitic habit has been ascribed to this fungus, but as yet there is no positive evidence to substantiate this view. The organism is characterized by spores which consist of four large, dark-colored, echinulate cells arranged in two opposite pairs, these pairs being separated by two smaller, light-colored, smooth-walled centrally located cells forming an isthmus (fig. 1, D; 2, C,D,E) between the two pairs of larger cells. Between the two larger cells, slightly above them, and on opposite sides of the central isthmus are two subglobose, smooth-walled, lighter-colored cells (fig. 1, E; 2, C,D,E); and below the isthmus is a single central, hemispherical, lighter-colored, smooth-walled cell which attaches to the hypha bearing the spores (fig. 2, C,D,E). I have been able to find no spores still attached to their conidiophores; and I have seen only mature spores, so that the ontogeny of this curiously shaped spore cannot be discussed at this time. Examination of descriptions as well as type material of

meliolicola, type. × 1500. E. Spores of *Isthmospora spinosa*, type. × 1650. F. Stages in ontogeny of spores of *S. tessarthra*, QM 371c. × 1500. G. Spores of *S. tucumanensis*, type. × 1500. H. Spores of *Sporidesmium tessarthrum*, type. × 1500. I. Spore of *S. tucumanensis*, type, showing orientation of echinulate spores on conidiophore. × 1500. J. Spores of *S. tucumanensis* type, showing small, smooth-walled spore and large, echinulate spore in face view. × 1500. Drawings made at specified magnifications and reduced ½.

all of the species mentioned above except *S. meliolae* (the type of which seems to be lost), shows them all to be identical; and from the number of species based upon the same organism described as belonging to *Spegazzinia*, there seems to be a strong tendency to disregard *Isthmospora* and to place this species in *Spegazzinia*. Despite the superficial similarity in morphology of spores of *I. trichophila* and *S. tessarthra*, the more complex spore morphology of *Isthmospora* and its association with *Meliola* seem to me to indicate a generic difference between these organisms. Furthermore, it is felt that the undescribed species referred to *Spegazzinia* in a recent publication (Hughes 1952, p. 72) supports the thesis that there are probably several species in which the spore morphology is of the *Isthmospora*-type, and that these comprise a homogenous group of species quite distinct from *S. tessarthra*. For these reasons it is felt that *Isthmospora* should be maintained. Unfortunately, the very descriptive epithet applied by Stevens to the type species must give way to an older name proposed by Atkinson (1897), and the type of *Isthmospora* must be known as **Isthmospora trichophila** (Atk.) comb. nov. (published as *Spegazzinia trichophila* Atk., Cornell Univ. Bull. 3 (1) : 49. 1897). The other names mentioned here must go into the synonymy of this species; and in addition, *Tetrachia singularis* Sacc. and *Stemphylium muriculatum* Sacc. are probable synonyms. Sydow & Sydow (1921) stated that *Tetrachia singularis* Sacc. was a synonym of *S. meliolae* Zimm. and from Saccardo's (1918) description this may indeed be the case. The description of *S. muriculatum* Sacc. (Saccardo 1917) also suggests identity with *I. trichophila*. The type specimen of *S. coffeae* was examined, and only a few very collapsed spores were seen so that no illustration has been given for this species but there is no question of its identity with *I. trichophila*.

The second species of *Isthmospora*, *I. glabra*, was described (Stevens 1918) as having smooth-walled spores which were slightly lighter in color and somewhat smaller in size than those of *I. spinosa*. Authentic material (the type seems to be lost) borrowed from the New York Botanical Garden has made it possible to obtain some understanding of this species. The only fertile specimen (No. 8915) provided a few scattered and collapsed spores of the general appearance and dimension described for *I. glabra*; and close examination of these spores indicates that Hansford (1946) is probably correct in believing this species to be very much like his *Spegazzinia chandleri* (1943). I have not seen type material of Hansford's species and the difference in spore sizes may be decisive in separating the two species, but I do not believe that either can be placed in either *Isthmospora* or *Spegazzinia*. They are clearly congeneric and further study may warrant describing a new genus for them, but there is too little material available to allow this at the present time. These species are also very similar in appearance to *Aorate costaricana* Syd. [= *Titaea costaricana* (Syd.) Boedijn (1951)].

Spegazzinia effusa Karsten was described in 1884 (Karsten), and was transferred by von Höhnel (1911) to *Clathrococcum*. Examinaton of the type specimen of *S. effusa* Karsten reveals no trace of a fungus which might answer Karsten's description except for numerous perithecia of a species of *Melanomma* identifiable with *M. pulvis-pyrius*. There is no sign of any other fungus on this material, and the *Melanomma* is present in great abundance. Although this is probably the organism actually observed and described by Karsten, its identity cannot be proven because the spore measurements are smaller than those of his description, being only 15.4–16.8 × 4.2–4.9μ (35–42 × 18–22μ, Karsten 1884). It is my opinion that this should become a synonym of *M. pulvis-pyrius*, but since the evidence presented is not conclusive, *S. effusa* should be placed among the *species dubiae* of *Spegazzinia*.

Two other species, *S. lobata* (B. and Br.) von Höhnel and *S. calyptrospora* von Höhnel (von Höhnel 1902), may also be considered together. Examination of a slide of *S. calyptrospora* made from the type material of this species (fig. 2, B) shows spores (14–42 × 9.5–26μ) bearing no morphological similarity whatsoever to those of *S. tessarthra*. I am, therefore, excluding this species from *Spegazzinia* and referring it to the *"Sporidesmium"-Coniosporium-Papulospora* complex for consideration. A similar statement may be made concerning *S. lobata* (von Höhnel 1902) which, from its description and illustrations, produces dictyospores of rather irregular appearance, not at all like those of the type species of *Spegazzinia*. It is also excluded from the genus as defined here and referred to *"Sporidesmium"* for further consideration.

Another species to be excluded following an examination of its type and several authentic specimens is *Spegazzinia ammophila* Rostrup. This species was described from *Psamma arenaria* collected on Helgoland and is described and illustrated (Rostrup 1896) as producing dark-colored (45–80 × 8–16μ) dictyospores in sporodochia. Spores from the type specimen (fig. 2, A) confirm this except that measurements range from 19–32 × 12–17μ, and indicate that the organism belongs among the species attributed to the *Stemphylium-Macrosporium* complex rather than to *Spegazzinia*. I am at a loss to explain the discrepancy between Rostrup's measurements and those which I made, although I am sure the same fungus was studied by both of us.

Spegazzinia rubra Dearness and House is known only from its type collection on dead stems of *Polygonum scandens* from New York (Dearness & House 1923). Examination of the scanty material present on the type specimens shows it to have rough, subglobose dictyospores borne terminally on conidiophores aggregated in sporodochia of the type referable to *Epicoccum*.[2]

[2] Based upon examination of material in the Link herbarium, *Epicoccum nigrum*

I have included below descriptions of the single good species of *Spegazzinia* and of *Isthmospora*.

Spegazzinia tessarthra (B. and C.) Sacc., Sylloge Fungorum 4: 758. 1886.

Sporidesmium tessarthrum B. and C., Jour. Linn. Soc. 10: 355. 1869.

Spegazzinia ornata Sacc., Rev. Myc. 2: 140. 1880.

Spegazzinia tucumanensis Speg., Rev. Facul. Agron. La Plata 19: 256. 1896.

Tetrachia quadrigemina B. and C. ex Cooke, Grev. 12: 97. 1884.

Triposporium cristatum Pat., Bull. Soc. Myc. Fr. 4: 125. 1888.

Spegazzinia brasiliensis Speg., Bol. Acad. Nac. Ciencas 23: 538. 1919.

Sterile hyphae usually within the substratum, effuse, light-colored, septate, branching, fuscous when superficial; fertile hyphae simple, fuscous, erect or ascending, elongate or reduced to short branches of the vegetative mycelium, aggregated into sporodochia, although this character is somewhat less noticeable in cultures, sporodochia measuring 0.1–1.0 mm. in diameter, usually separate, rarely confluent; conidia borne singly and terminally as terminus spores on the fertile hyphae; conidia dark-colored, wider than thick, typically 4-celled with the four cells arranged in the form of a Maltese cross (most noticeable in immature or smooth-walled spores), spores of two types, one smooth at first becoming echinulate and the other remaining smooth-walled; spores sometimes variously shaped, muriformly septate spores also present, spores sometimes retaining small portions of the conidiophore when freed, smooth conidia 10–18μ in diameter (front view) and 5–9μ thick; spiny conidia 16.5–25.5 × 14–21 × 9–18.5μ.

Type locality: Cuba.

This species is common on decaying monocotyledonous plant parts in both New and Old World tropical and subtropical regions.

Since its original description, this species has been discussed in detail by Bessey (1907) and van Overeem (1923). Neither of these authors observed cultured material, but studied specimens from a large variety of substrata. In culture, this species produces a flocculose, white aerial growth on the surface of which may be seen somewhat irregular clumps of conidia borne on relatively short conidiophores. The conidia produced are, in all respects, like those observed in dried specimens.

The conidia shown in figure 2, F illustrate the manner of spine development in this species. After the basic cell plan of the spore has been laid down, the spines appear first as small protrusions at the basal angles of the triangularly shaped cells. One or more spines may appear, and are sometimes observed on one cell before appearing on others in the same spore, although the usual case is to find them developing simultaneously on all cells. As a rule, spines appear on the front surface of the cells and all begin to enlarge with those first formed attaining the greatest length and diameter. In mature spores large numbers of variously sized spines are found, the cells themselves have become rounded and much larger as evidenced by the larger size of the echinulate spores. In most instances, the conidiophores are short and form a

Link has been found to be identical with the organism known under the name, *E. neglectum* Desm., the spores of *E. nigrum* being dictyospores.

closely-appressed, cushion-like sporodochium; but in figure 1, B are shown the conidiophores and conidia of a loosely aggregated sporodochium as well as one of the typical form.

This species has a tropical and subtropical distribution and is usually found as minute, black sporodochia on decaying plant parts, especially grass leaves and stems. It has also appeared in isolations made from tentage and from cardboard (QM 371e, 373c, 840, and 841). In laboratory tests, cultures of this species cause 53–97% loss of tensile strength of duck strips and 40–69% loss of strength of wool strips indicating that it possesses moderately strong keratinolytic as well as cellulolytic activity.

Isthmospora trichophila (Atkinson)

Isthmospora spinosa Stevens, Bot. Gaz. 65: 244. 1918. ill.
Spegazzinia trichophila Atkinson, Bull. Cornell Univ. 3(1): 49. 1897.
Spegazzinia meliolae Zimmermann, Cent. f. Bakt. II: 8: 221. 1902.
Spegazzinia meliolicola Hennings, Hedwigia 43: 398. 1904.
Spegazzinia coffeae Hennings, *apud* De Wildeman, Mission E. Laurent 3: 318. 1906.
?*Tetrachia singularis* Saccardo, Boll. Ortho. Bot. R. Napoli 6: 65. 1918.
?*Stemphylium muriculatum* Saccardo, Att. Accad. sci. ven.-trent. 10: 86. 1917.

Sterile hyphae superficial, effuse, fuscous, septate, branching, inconspicuous, hypophyllous and intermingled with the hyphae of species of *Meliola;* fertile hyphae short, simple, reduced to branches of the vegetative hyphae, septate or not; conidia borne singly on these branches as terminus spores, dark-colored, multiseptate, having a rectangular appearance; conidia composed of two pairs of large, dark-colored, echinulate cells separated from each other by two pairs (upper and lower) of smaller, lighter colored, smooth-walled cells, and by two central cells (the isthmus); below the "isthmus" cells is a single subhemispherical, centrally located cell to which the conidiophore is attached; conidia 14–23 × 11–18.5μ in length and width and 8–12.5μ in depth.

Type locality: Auburn, Ala., U.S.A.

This species has been found associated with a large number of species of *Meliola* on various hosts in tropical and subtropical regions, and appears to be restricted to these regions in both hemispheres.

SUMMARY

1. In this investigation, the intention has been to examine the known species of *Spegazzinia* from as many type specimens as possible because it is only in this manner that it will ever be possible to know them properly. For instance, without reference to type material there could always be some doubt as to the actual identity of *S. trichophila, S. meliolicola,* and *I. spinosa.* Because I was able to study type material, however, this difficulty is obviated and support is derived for the opinion that *S. meliolae* and others are also identical with *I. spinosa* although their types have not been available for study.

2. Of the described species, *S. brasiliensis* Speg. and *S. chandleri* Hansford have not been studied from specimens. *S. chandleri,* though not seen, is known from Hansford's clear description and illustrations; and the type of *S. brasiliensis* appears to be lost (Lindquist, personal communication). It is hoped that these considerations may serve as a basis for monographic work in this genus, and that they may serve to broaden our understanding of some less well-known genera of Hyphomycetes.

ADDENDUM

Another species of interest here appeared on a specimen found in Puerto Rico on sugar cane labelled *S. ornata.* It is identical with the type material of *Tetracoccosporium sacchari* Stevenson. *T. sacchari* has been discussed recently by Hughes (1952) in connection with his *Dictyoarthrinium quadratum* and was considered "only critically distinct from the African fungus" *(D. quadratum).* Examination of Stevenson's type material and comparison with Hughes's excellent illustration and description make it difficult to see how the two species could be maintained distinct. Comparison of Stevenson's specimen with Hughes's figures show that the conidia and conidiophores are the same, the only difference between the species being that the spores of the Stevenson type have slightly coarser tubercles and that both of the American specimens have appeared on sugar cane. In American and African specimens, however, the substratum is monocotyledonous; and for this reason it is felt that the older name, *T. sacchari,* should replace *D. quadratum* and the species should be disposed as follows:

Dictyoarthrinium sacchari (Stevenson apud Johnston and Stevenson), comb. nov.

Tetracoccosporium sacchari Stevenson apud Johnston and Stevenson, Jour. Dept. Agr. Porto Rico 1(4) : 225. 1917.

Dictyoarthrinium quadratum Hughes, Myc. Paper (C. M. I.) No. 48 : 30. 1952.

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CAUSES OF DEATH OF PLANTS AS A CONSEQUENCE OF LOSS OF WATER: CONSERVATION OF LIFE IN DESICCATED TISSUES[1]

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From the standpoint of their response to water loss, plants may be divided into two basic groups: (1) species which are capable of conserving themselves in dry air even though deprived of water for extended periods. In this group belong certain species of lower plants and those which survive by means of spores and seeds; and (2) species which die as a consequence of wilting and partial desiccation. Vegetative tissue cells of the majority of ordinary green plants belong in this group.

The cause of differential drought resistance is attributed generally to the presence of special substances, such as certain colloidal substances and sugars, which protect the protoplasm against dehydration and consequent coagulation. Death of cells whether as a consequence of drying or of freezing presents certain similarities. As the investigations of certain workers (Lidfors 1907, Maximov 1912, Schander and Schaffnit 1919) have shown, increase in tolerance to freezing is accompanied by an increase in sugar content of the tissues. A period of drought stimulates the accumulation of sugars.

In the experiments of Maximov (1912) tissues placed in sugar solutions tolerated temperatures much lower than those in water or in air. Iljin (1927) in studying the effects of dehydration obtained similar increased tolerance. The writer's present studies of responses to dehydration deal with cellular changes following plasmolysis, deplasmolysis and coincidentally-occurring phenomena, as related to the maintenance of life by the tissues.

Methods. Graduated series of known concentrations of glucose, sucrose, and sodium chloride were prepared for use as agents to induce plasmolysis and deplasmolysis. As an alternative means to this end, and in some instances as a supplementary one, desiccators were employed. Into the basal portions of these desiccators were placed differing concentrations of sulphuric acid to provide for maintenance of differing constant relative humidities of the atmosphere above the layer of acid. Free-hand sections of tissues of the different species of plants or strips of tissues to be dehydrated were immersed in a portion of the stock solutions, passing the tissues seriatim

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from the less concentrated to the more concentrated ones during plasmolysis and reversing the order of passage in deplasmolysis. The desiccators providing atmospheres of differing relative humidities were similarly used to dehydrate or to rehydrate the tissues. In any event survival of cells was adjudged by return of the protoplasts to their normal positions, after the cells had been plasmolyzed.

Protective action and concentration. Leaf tissues, previously submerged in neutral salt solutions or in sugar solutions, were placed in chambers of differing relative humidities, relative humidity being controlled by varying the concentration of sulphuric acid in the chambers. By this technique, green leaf tissues of iris, previously placed in water, died when placed in an atmosphere having a relative humidity of 97%, whereas those previously placed in salt or sugar solutions died if the relative humidity was maintained at 90–93%. Similarly the cells of *Rhoeo discolor* died when placed in an atmosphere of 99% relative humidity; but if the tissues had previously been placed in 0.1 N glucose, they died only when the relative humidity was lowered to 96%, and tissues previously placed in 1.0 N solution survived in an atmosphere of 87.5% relative humidity. Apparently these experiments establish the hypothesis that such substances exert a protective action against desiccation. If these solutions consist of non-electrolytes they exercise greater protection. On the other hand, if these solutions consist of high concentrations of electrolytes they produce injury and decrease the tolerance.

A vegetative cell is delimited by a very delicate protoplasmic layer and within the interior is a large water vacuole. When this water is withdrawn from the cell, the volume of the vacuole decreases, the protoplasm and the plasma membrane are similarly affected and the cell is strongly contracted (Schroeder 1886, Steinbrinck 1900, 1903 and 1906, Holle 1915, Thoday 1918). The protoplasm may not separate from the cell wall and plasmolysis is not produced. My numerous observations (Iljin 1927, 1930 and 1933) completely confirm the occurrence of these events during dehydration of the cell. Considerable tension may arise between the wall and the protoplasm; consequently at times the protoplasmic layer is ruptured and its fragments remain along the walls. These processes in reverse sequence are produced when partially desiccated cells are placed in water. The vacuole imbibes water and increases in volume; the membrane swells and the protoplast is dilated. Tissues which have lost only a small quantity of water reestablish their turgor and remain alive. If the loss was very large, however, the cells will die as shown by their failure to deplasmolyze.

By submerging tissues in solutions of sugar or salts, one can ultimately cause them to lose a large quantity of water without killing them if they are plasmolyzed gradually. It is necessary to submerge the tissues first in weak

solutions, then to pass them to more and more concentrated ones, and then to deprive them of more of their water by placing them in chambers with different relative humidities. Using tissues thus gradually dehydrated, it is necessary in restoring water, to place them first in a concentrated solution and then in a series of less and less concentrated ones, because the cells die if placed directly in water.

By using the method just described, one can maintain the tissues of plants which are very sensitive to desiccation in a dehydrated condition for a long time. The cells of *Rhoeo discolor,* for example, are very sensitive to dehydration, and as previously stated, die when placed in an atmosphere of 98–99% relative humidity. In my experiments, however, sections were first plasmolyzed and then placed in microchambers of different relative humidities, where they were kept for as long as 21 days. After having been dried in this way the tissues were then passed through a series of solutions, first concentrated ones and afterwards more dilute ones. When this was done the cells were alive not only after desiccation in an atmosphere of 90% relative humidity but also when it was lowered to 60–65%. The epidermal cells of red cabbage, when similarly treated, were alive after remaining desiccated for 6 days in an atmosphere of 40% relative humidity.

As a next step, desiccation was continued until water was completely eliminated by exposure to the drying action of concentrated sulphuric acid in chambers. The epidermis of *Rhoeo discolor* was gradually dehydrated in chambers of progressively lower relative humidities during a period of 10–11 days, and then exposed to dry air over concentrated sulphuric acid where it was allowed to remain for 8–14 days. Even after complete drying in this manner, many of the cells were found to have survived. After gradual desiccation in the same way the epidermis of red cabbage was found to have conserved life for 60–72 days, and in one experiment for four months. Also the parenchyma cells of roots of *Beta vulgaris* were alive after 55 days over concentrated sulphuric acid, and the leaves of *Mnium undulatum* after four months. Cells in a dry condition have a high degree of tolerance, and in this state can be heated at a temperature of 72° C for 24 hours without killing them. However if the temperature is raised to 100°, they are killed within a short time.

Death of cells from plasmolysis and deplasmolysis. One of the principal factors inducing death of cells is the change in structure of the protoplasm in the process of loss and recovery of moisture. The cells shrink and swell as a consequence of decrease and increase in size of the vacuole. When the vacuole is large, the disturbances within the protoplasm are large. Various physical agents such as pressure, swelling, blows, etc., destroy the protoplasmic structure and cause death, as Lepeschkin (1938) showed in his numerous studies. Both plasmolysis and deplasmolysis, especially when

repeated, also provoke the destruction and death of the protoplasm (DeVries 1885, Lepeschkin 1938). Plants differ in ability to withstand plasmolysis, which in turn is dependent upon the structure of the protoplasm and upon the influence of constituent salts and acids, and of other physico-chemical factors.

The size of the cell plays a significant role in tolerance to plasmolysis and deplasmolysis. In large cells there occurs a greater change in the plasmolyzed protoplast than occurs in small cells when they are transferred to water and are deplasmolyzed. The experiments of Iljin (1934) showed the comparative results with 27 kinds of tissues. Osmotic pressure and volume were determined. The tissues were submerged in saccharose solutions of differing concentrations and afterwards were placed in water. Calculations show that the absolute osmotic pressure value is without influence upon the tolerance of cells, but the magnitude of change influences recovery of the plasmolyzed protoplast. In cells of volume greater than 75,000 μ^3 the protoplasm dies if the volume is increased 1.6 to 1.8 times. If, however, the cells have a volume less than 10,000 μ^3, they die if the volume is increased 4 to 5 times. Cells of intermediate size perish when volume increases have values of 2.3, 2.7, or 3.5 times.

The protoplasm suffers very appreciable injury when repeatedly plasmolyzed and deplasmolyzed. The injury is cumulative and finally a condition is reached when death ensues after only a slight change in turgor. In the following table are shown the osmotic pressure values of cells in tissue sections, the concentrations at which death of the protoplasts of green mesophyll tissues occurred after having been passed from sugar solution to water, and the number of such treatments.

TABLE 1. *Plasmolysis and deplasmolysis as related to survival.*

Species	Osmotic pressure, normal tissue, N	Concentration at which death ensued, N				
		Number of treatments:				
		1	2	3	5	7
Sedum purpureum	0.17	0.35	0.30	0.30	0.25	0.20
Sempervivum soboliferum	0.17	0.40	0.30	0.25	0.25	0.20
Cirsium canum	0.42	0.75	0.75	0.75	0.30	—
Poa badensis	0.62	1.5	1.2	1.2	1.0	0.8
Festuca glauca	0.60	1.5	1.0	0.8	0.8	0.7
Thymus serpyllum	0.43	1.2	1.0	0.7	0.6	0.5
Centaurea scabiosa	0.75	2.0	2.0	1.5	1.2	1.0
Anthericum ramosum	0.60	2.0	1.0	1.0	0.8	0.5
Syringa vulgaris	0.88	2.1	1.2	1.2	1.0	1.0

The cells tolerated the first plasmolysis well and were able to lose one-half to two-thirds of their water without injury. In the second plasmolysis

the majority of the species lost tolerance to a slight extent. With further repetitions there is increasingly greater loss of ability to recover, and after 5–7 plasmolyzations, the tissues will plasmolyze weakly or may have completely lost this response ability.

Effect of change of turgescence. Green parenchyma tissues of leaves were placed over sulphuric acid in air of differing relative humidities. Each day the tissues were wetted and immediately returned to the same relative humidity chamber. The following table shows the relative humidity at which protoplasts were killed.

TABLE 2. *Effect of repeated changes in turgescence.*

Species	Relative humidity at which the cells die				
	Number of moistenings or wettings				
	1	2	3	4	5
Cirsium canum	95	96	96	97	99
Bupleurum falcatum	90	92	95	—	97
Teucrium montanum	94	—	97	100	100
Thymus serpyllum	96	—	97	100	100
Rumex acetosa	96	96	99	99	99
Syringa vulgaris	89	91	92	—	94
Buxus sempervirens	90	91	92	92	92
Festuca glauca	90	—	92	92	94
Poa badensis	90	—	92	92	94

As a control, tissues were allowed to remain in a dry atmosphere for 5 days, and their cells remained alive. Tissues which were wetted every day and again dried daily declined in tolerance. Tissues of *Teucrium montanum* and *Thymus serpyllum,* wetted and dried three times, died in an atmosphere of 100% relative humidity. Similar results had been obtained by submitting them to plasmolysis. On the other hand, tissues of such other plants as *Buxus sempervirens, Festuca glauca,* and *Poa badensis,* when wetted and dried 5 times, showed little change in tolerance. These results indicate that different species of plants differ in ability to withstand changes in turgor. Presumably repeated changes in turgescence due to transpiration may produce similar loss of ability to recover.

Changes in desiccated tissues. Loss of water changes the consistency of the protoplasm making it more condensed and less responsive; and after each plasmolysis, return of the protoplast to its initial position is made more and more difficult. For example, the cells of red cabbage, having an osmotic pressure of 0.3 N, were submerged in sugar solutions of different concentrations for different periods. When transferred to water, they remained alive if they had been in a 1.2 N solution for only an hour; if they had been left in such a solution for 3 hours, they died on being returned to water, even if passed through a 0.5 N solution.

In cells partially desiccated in a relatively moist asmosphere without plasmolysis, the protoplasm swells after passage to water, as does the plasma membrane and the cell remains alive. In cells more severely desiccated, the protoplasm condenses and is made less mobile. Then the plasma membrane, after entrance of water, swells very quickly and separates from the protoplast which has shrunken in the center of the cell, producing the phenomenon of pseudoplasmolysis. Gradually the protoplast imbibes water and acquires a rounded form until it dilates to touch the walls. Depending upon the degree of desiccation, imbibition and swelling proceed very rapidly or very slowly. Sometimes it is accomplished in seconds or in a few minutes, and sometimes one to two and one-half hours are required. When tissues are deprived of water to a moderate degree, the membrane recovers first; finally the protoplast touches the wall and the cells continue to be alive. In tissues dried in an atmosphere of low relative humidity the protoplasts imbibe very little, and the majority of them disintegrate and die during swelling. If desiccation is very drastic, the cells die immediately without pseudoplasmolysis. In such cases rapid swelling of the membrane in water can result in disintegration of the protoplast.

In the foregoing experiments the principal cause of death of the dehydrated cells was derrangement in structure of the protoplast occasioned by imbibition and by rapid distention. If one impedes or slows down these processes, the cells will remain alive. For this purpose concentrated solutions, especially of saccharose (Iljin 1933), are found to be very useful. In so doing, tissues subjected to atmospheres of very low relative humidity should be transferred to the most concentrated solutions; those subjected to a moderate relative humidity, to solutions of intermediate concentration.

Recent investigations reveal that cells desiccated quickly in dry air are more easily killed than those dried gradually. Gradual desiccation requires that they be first placed in a relatively humid air and afterwards be passed gradually into drier air. The protoplast can be destroyed eventually by drying even if the membrane is very firm and resistant. Similarly cells conserve life better if they are gradually changed from a dry condition to a more humid one. For example, sections of red cabbage and of *Cirsium canum* were dried for 2 days in microchambers above solutions of NaCl of differing concentration. Those dried over a 0.5 N solution, when transferred to water, remained alive; those dried over a solution of 1.0 N at first showed pseudoplasmolysis but died afterwards; those dried over 2.0 N solution, when placed in water, died without pseudoplasmolysis. But if the tissues were placed in successively weaker concentrations of NaCl and finally in water, then the cells remained alive and were able to recover their turgor.

The tissues of red cabbage remain living and completely recover turgescence after being dehydrated in an atmosphere having a relative

humidity of 80% or less, if water is restored gradually. But the cells die if, after dehydration, they are placed immediately in an atmosphere of 98% humidity or if they are placed directly in water. Green leaf tissues of *Bupleurum falcatum* can be dried to a 50–55% relative humidity. They can remain in the dry condition for 4 weeks and can be revived by using the method of adding water progressively.

Specific differences in tolerance. The tolerance of different species of plants to desiccation differs greatly, as is apparent from the following experiments in which different methods of dehydration were used.

Effect of rapid dehydration. Small sections of leaves were desiccated in air having a relative humidity of 55–60%. They became desiccated quickly and were permitted to remain thus for different periods of time. In table 3 are shown the duration of the periods employed and the approximate percentage of living cells.

TABLE 3. *Survival of different species after rapid desiccation for differing periods.*

Species	Duration of the desiccation period	Percentage of living cells
Bupleurum falcatum	6 hours	100
" "	2 days	76
" "	6 days	10
Berteroa incana	21 hours	100
" "	2 days	100
" "	6 days	few
Syringa vulgaris	1 hour	100
" "	6 hours	few
Buxus sempervirens	1 hour	100
" "	6 hours	few

Such treatment is very harsh, and the tissues of the majority of the species tested died. However, some species survived such treatment.

Effect of gradual dehydration. Tissues were gradually dried to that of an atmosphere of 70% relative humidity and then allowed to remain in the dry air of the laboratory. By this method the cells remained alive longer than when rapidly dried as may be seen in the following table.

TABLE 4. *Survival of different species after slow desiccation for different periods.*

Species	Duration of the desiccation period	Percentage of living cells
Bupleurum falcatum	8 days	100
" "	10 days	72
" "	4 weeks	50
Syringa vulgaris	2 days	100
" "	4 days	50
" "	6 days	few
" "	8 days	0

Both species (table 4) show greatly increased tolerance when desiccation is effected gradually but the other species tested were not found to differ significantly. Tissues of *Berteroa incana* showed slightly more tolerance but finally succumbed after 10 days. The cells of *Buxus sempervirens* were able to remain alive in a dried condition but differed greatly among themselves in tolerance to drying. Some could tolerate drying for a few hours, some for a few days, and others for a period of weeks or months.

Cell size and shape as related to survival. The size of the cell, as previously indicated, is of great importance in tolerance to drying. The larger the cell, the more space the vacuole occupies, the less the tolerance. Many investigators have noted that the cells of plants of dry regions are smaller than those of wet locations (Stahl 1883, Dufour 1887, Nordhausen 1903; 1912, Kolkunov 1905; 1925, Rosé 1913, Rippel 1919, Maximov 1929). Very drought-resistant mosses have a cell volume of 300–700 μ^3, sometimes 100–200 μ^3 or even as small as 50 μ^3; although the cell volume of higher plants may be as great as 1–3 million μ^3.

My own measurements of cells in the fresh condition and the dried one (Iljin 1930) show that the volume of small cells may be decreased 1.8–2.0 times and that of large ones 5–10 times, the larger cells being the more greatly affected.

Grebe (1917) showed that xerophytic mosses survive when dried in a desiccator over concentrated sulphuric acid. Such mosses have a cell diameter of 3–4 μ, rarely 7 μ, although the cell diameter of higher plants may be 80–150 μ.

The shape of the cell is also a factor. Small cells with pronounced differences between length and width are more tolerant than are large spherical or cubical cells. The greater the volume and the less the surface area, the less tolerant is the protoplast; that is, the volume/surface ratio is one of the factors which determines tolerance (Iljin 1930). The stem of *Sinningia purpurea*, as that of many other plants, has large cells at the center with an average volume of 1,200,000 μ^3 and a V/S ratio of 17. The cells near the periphery have a volume of 224,000 μ^3 and a V/S ratio of 9. The osmotic pressure of both cell groups is equal to 0.2 N. But the former die in an atmosphere of 99% relative humidity and the latter, of 96%. Similarly the central cells of stems of *Amaranthus verschaffeltii* have a volume of 1,200,000 μ^3 and a V/S ratio of 19; the small peripheral cells, a volume of 160,000 μ^3 and a V/S ratio of 7. The osmotic pressure of both kinds varies between 0.3 N–0.4 N. The former die at 97% relative humidity and the latter at 93%.

Osmotic pressure, absorptive power, and relative humidity. Plants growing in dry sites are characterized by having cell sap of high osmotic pressure. To a certain extent this factor favors the plant with respect to drought. Cells having a sap concentration of 0.25 N may lose half of their

water when placed in an atmosphere of 99% relative humidity, as this humidity corresponds with a solution of 0.5 N. Cells with an osmotic pressure of 1.0 N may be expected to maintain their turgor in an atmosphere of 98% relative humidity.

In the following experiments 70 different plant tissues were studied. The relative humidity at which the cells died was determined. The osmotic pressure, volume, surface, and absorptive power of the cells were also determined using the method of Walter (1930). The relative humidity at which cells die when transferred to water as related to osmotic pressure of the sap is shown in the following table.

TABLE 5. *Influence of osmotic pressure of sap upon tolerance to drying.*

Osmotic pressure of sap, normal	Relative humidity at which cells die, per cent
0.2	99
0.26–0.35	97–96
0.4 –0.55	94–92
0.5 –0.6	92
0.65–1.0	90–98

When the 70 kinds of plant tissues were grouped according to osmotic pressure of the cell sap, there is shown a direct correlation with tolerance to relative humidity.

The table which follows shows correlation between cell tolerance and absorptive power calculated according to Walter's method.

TABLE 6. *Correlation of absorptive power and relative humidity.*

Absorptive power in atmospheres	Relative humidity at which cells die, per cent
14	99
40–50	97–98
95–142	93–90
181	87.5

Small cells with osmotic pressure of 0.2–0.3 N, which corresponds to 8–14 atmospheres, are able to survive in an atmosphere of 93% relative humidity when the absorptive power is increased to 96 atmospheres. The cells of *Buxus sempervirens, Hedera helix* and *Pinus sylvestris*, falling in the group with an osmotic pressure of 0.85–1.0 N or of 27–34 atmospheres absorptive power, survive in an atmosphere of 90–87.5% relative humidity when the absorptive power is increased to 142–181 atmospheres.

Discussion. The conservation of life by cells or by organisms that have been dehydrated has long been a subject of investigation. As a result a

large body of data of physiologic and ecologic importance bearing on hydration and dehydration has been accumulated. These data show the occurrence of many correlated structural and chemical modifications which control and accompany both conservation and loss of water.

In a recent ecologic study Arvidsson (1951) suggests that in plants two types of tolerance or resistance to desiccation be recognized, active and passive. Primary active resistance involves ability of the tissues to tolerate desiccation and secondary active resistance, to avoid or escape desiccation. Passive resistance involves ability to pass into a dormant stage.

It would appear that there are no fundamental differences between the protoplasm of different species with respect to dehydration. In this study a principal cause which favors death following dehydration is related to the presence of a large vacuole containing a large quantity of water. The protoplasmic structure of such cells may be greatly damaged by hydration and dehydration.

Leaf buds of some plants exhibit a striking tolerance to drying. The cells of their tissues either lack vacuoles or have very small ones. But during growth the vacuoles increase in size and coincidentally there is a decrease in tolerance to dehydration. Similar changes have been noted during germination of seed and subsequent development of seedlings.

Encystment and endospore formation as occur in certain lower organisms function in defense against periods of drought. Similarly spores, lichen thalli, and the cells of seeds and certain mosses become filled with reserve foods which function protectively against desiccation. In such cells, vacuoles may be completely wanting.

Although size of the cell and vacuole are herein regarded as important factors in conserving life in plant tissues, the osmotic pressure of the sap, differing with the species, must also be taken into consideration.

SUMMARY

1. Plant tissues that have been dehydrated may conserve life for long periods, indicating that desiccation itself may not be the cause of death of the protoplasts. Rate of dehydration and rate of restoration of water are found to be critical factors for survival of protoplasts of desiccated tissues.

2. Vegetative tissues conserve life if dehydrated slowly and can be made to tolerate the loss of a large proportion of their water. In extreme cases they may be made to tolerate drying over concentrated sulphuric acid for weeks or even months. They die, however, if dried quickly and if permitted to recover their water quickly.

3. Recovery from repeated plasmolysis and deplasmolysis becomes increasingly difficult and eventually death results when the cells are exposed to change in turgor.

4. In cells that possess large vacuoles, plasmolysis and deplasmolysis cause a greater amount of contraction and swelling of the protoplasts than in cells with small vacuoles. Shrinking and swelling, whether once or more often, may provoke profound disturbances in protoplasmic structure.

5. Different species of plants differ greatly in tolerance to desiccation. Differences in cell size, cell shape, ratio of volume to surface area, and osmotic concentration of sap are correlated with differences in tolerance.

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A NEW MEMBER OF THE PHACOTACEAE

HAROLD C. BOLD AND RICHARD C. STARR

The Phacotaceae include those motile, unicellular Volvocales whose cells are enclosed in a wall-like envelope, the lorica, which may be separated by some distance from the surface of the protoplast. The lorica may be hyaline in young cells, but in older individuals, it is often colored brown by the deposition of iron compounds or variously ornamented with calcareous granules. Species of eight genera of Phacotaceae have been reported to occur in the United States (Smith 1950).

The organism here described, which is a member of the Phacotaceae, was collected in August 1951 in small rock pools along the old bed of the Caney Fork River at Rock Island, Warren County, Tennessee. The main flow of the river has been diverted into a flume at that locality, so that the rock pools where the organism occurred are filled with rain water during the summer, whereas they may be submerged by high water during the winter months. In several pools, the plant developed in such large numbers as to color the water cinnamon-brown; the bloom appeared like one composed of the euglenoid, *Trachelomonas*, which the alga, here to be described, superficially resembles. The organisms have been maintained since their collection in soil-water culture media according to the method of Pringsheim (1946); they grow and reproduce rapidly in such media at a temperature of 22° C., when illuminated at an intensity of 100 footcandles for twelve hours daily with light from a fluorescent fixture. Clonal and unialgal cultures of this organism have been obtained in liquid media; growth on solid media of various types has so far been negligible. The observations reported below are based on study of living cells in hanging drop preparations and of smeared preparations, stained with Haidenhain's haematoxylin after fixation in LaCour's 2BD fluid (Johansen 1940) and Schaudinn's solution (Gatenby and Painter 1937). A careful appraisal of its morphological attributes and comparison of them with those of other genera of Phacotaceae have convinced the writers that the organism should be classified as a hitherto undescribed species of the genus *Dysmorphococcus* Takeda. The specific characters are as follows:

Dysmorphococcus globosus Bold and Starr, sp. nov. Lorica spherica, ad 28 μ diam., sine colore in cellulis iunioribus, luteo-fusca in cellulis vetustioribus, reticulo irregulari areolarum punctatarum ornata; papillam, a latere visam hemisphericam, atque daus aperturas flagellares habens.

Protoplastus sine membrana, loricam nisi in tempore propagationis non implens. Chromatophorus urceolatus, in cellulis vetustioribus in multas partes interdum partim fissus. Pyrenoidea vacuolaeque pulsantes multae,

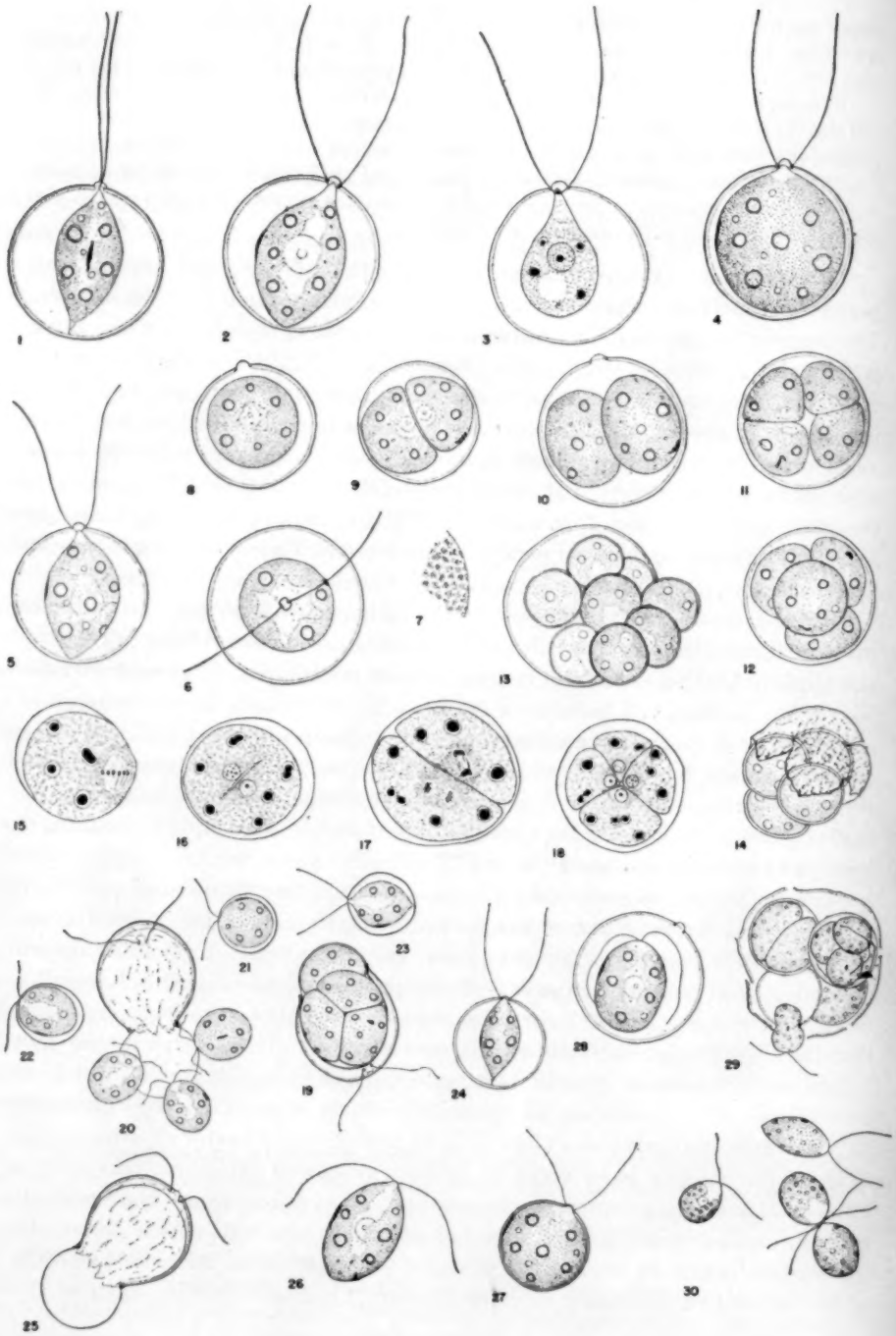
usque ad quindecim; stigma lineare in chromatophoro aequatorium. Nucleus centralis. Papilla plasmatis sine colore, duo flagella ferens. Flagella paulo longiora quam diametros loricae. Planta proprietatibus ceteris generi similis.

Propagatio per zoosporas quattuor, in lorica-matre formatas. Flagella cellulae-matris tempore propagationis persistentia. Zoosporae, e loricae parte posteriore liberatae, stratum membranae interius velut vesiculam extrahentes. Aplanosporae necnon formatae, usque ad sedecim omnibus in cellulis. Aplanosporae maturae luteo-rubrae, in unam vel quattuor zoosporas, velut gametae potentiales fungentes, germinates.

Observations. Mature individuals of *D. globosus* are, as a rule, almost perfectly spherical (figs. 1–6) and may attain a diameter of 28 microns. The flagella length slightly exceeds the diameter of the lorica. The latter is thin and hyaline in young cells (figs. 22–24, 31, 32) but darkens as the cell ages. The lorica increases in thickness in older cells; its outermost layer is apparently smooth, but the inner layers are ornamented with an irregular, mosaic-like pattern of brownish granules (fig. 7). No evidence of pores, such as have been detected in *D. variabilis* Takeda (Bold 1938), could be observed in the loricas of *D. globosus*. The iodine and sulphuric acid test for cellulose was negative, when applied to loricas of both young and mature individuals.

The anterior (flagellated) pole of the lorica bears a prominent papillate protuberance, which appears almost hemispherical in lateral view (figs. 1–5) and slightly bilobed at its base in frontal view (fig. 6). Its roughened surface, which can be observed more readily in some individuals than others, indicates that it is probably an eversion of the inner layers of the lorica. In polar view (fig. 6), the base of the papilla may be seen to be interrupted by the two flagellar apertures, which are oriented relative to each other at an angle of 180°. The papilla is persistent in old loricas whose protoplasts have been lost through reproduction (fig. 25).

The protoplast is bounded only by a plasma membrane and not by a cellulose wall layer. This fact has been directly established through the use of plasmolytic agents and by iodine and sulphuric acid; it is indirectly indicated by the observed capacity of the protoplast to undergo changes in form (figs. 1, 3, 4, 9 and 29) during reproduction. There is evidence, however, that the daughter protoplasts are surrounded by a common membrane just before their liberation (fig. 19); the exact origin of this layer has not been ascertained. The protoplast of most individuals is attenuated at both the flagellar and posterior poles (figs. 1, 5, 31 and 32); the posterior attenuation in some individuals is so great as to appear almost stipitate. However, a number of actively swimming cells has been observed in which the posterior pole is rounded (figs. 2, 4) and separated from the wall of the lorica. In the writers' opinion, separation of the protoplast from the posterior pole of the lorica is a precursor of reproduction. That neither the lorica or the



protoplast is compressed is clear in anterior polar view (fig. 6).

The anterior extremity of the protoplast forms a protoplasmic papilla which protrudes slightly into the lorica papilla (figs. 1–5). The two flagella are attached a short distance back from the apex of the protoplasmic papilla. In some stained preparations, there is good evidence that they emerge from a deeply staining blepharoplast (fig. 3).

The chloroplast is urn-like, with a rather small anterior opening. In most individuals, it is relatively smooth and homogeneous, but in occasional cells (fig. 5) it appears to be partially cleaved about the several pyrenoids. The latter, twelve or more in number, are embedded near the surface of the chloroplast; in actively moving, well illuminated cells, the pyrenoids usually are surrounded by starch envelopes. Each cell possesses a single prominent equatorial stigma embedded in the chloroplast near the plasma membrane (figs. 1, 2, 5 and 6). The stigma is streak-like in form in mature cells, but in younger cells it is less regular (figs. 19, 20). A number of contractile vacuoles occurs, quite evenly distributed over the surface of the photoplast (figs. 1, 5); these are difficult to observe in individuals filled with starch and other metabolites. From optical sections (figs. 2, 6) and stained preparations (figs. 3, 15) it is clear that the lumen within the chloroplast is filled

FIGS. 1–30 were drawn with the aid of a Leitz camera lucida. The approximate magnification is given for each figure. FIG. 1. Mature vegetative individual, surface view; note numerous contractile vacuoles. × 925. FIG. 2. Mature vegetative individual, median optical section; central nucleus and flagellar apertures visible. × 925. FIG. 3. Fixed and stained vegetative individual; nucleus, pyrenoids and blepharoplast visible. × 925. FIG. 4. Vegetative individual just prior to formation of daughter cells; protoplast almost fills the lorica; numerous contractile vacuoles visible. × 925. FIG. 5. Vegetative individual with partially dissected chloroplast, surface view. × 925. FIG. 6. Anterior polar view combined with median optical transverse section of one vegetative cell. × 925. FIG. 7. Portion of lorica of mature cell, surface view. × 1200. FIGS. 8–14. Aplanospore formation and liberation in living specimens. FIG. 8. Protoplast has become spherical, flagella absent. × 675. FIG. 9. Conclusion of first bipartition. × 675. FIG. 10. Slightly later stage than 9. × 925. FIG. 11. Conclusion of second bipartition. × 675. FIG. 12. Four young aplanospores, as yet unwalled, two with stigma. × 675. FIG. 13. Eight aplanospores being liberated by coverglass pressure. × 925. FIG. 14. Natural liberation of four aplanospores. FIGS. 15–18. Formation of zoospores from stained preparations. FIG. 15. Metaphase of first mitosis; note pyrenoid elongating. × 675. FIG. 16. Interphase and cytokinesis; note pyrenoid divisions. × 675. FIG. 17. Late anaphase and telophase of second mitosis, approximately 10 chromosomes visible. × 675. FIG. 18. Interphase following second mitosis and cytokinesis. × 675. FIG. 19. Early stage in liberation of four motile daughter cells (zoospores); note persistent flagella of parent cell. × 675. FIG. 20. Liberation of zoospores, fourth zoospore below, not illustrated; note hyaline vesicle to which zoospores are attached by the proximal portions of their flagella. × 675. FIGS. 21–23. Young vegetative individuals at twenty minute intervals after they became detached from hyaline vesicle. × 675. FIG. 24. Young vegetative individual, 24 hours later. × 925. FIG. 25. Old lorica with persistent flagella and hyaline vesicle, 48 hours after liberation of zoospores. × 675. FIG. 26. Individual released from lorica by mechanical pressure. × 925. FIG. 27. Young individual, product of germination of an aplanospore. × 925. FIG. 28. Individual with flagella withdrawn into lorica. × 925. FIG. 29. Germination of previously desiccated aplanospores into gamete-like swarmers. × 925. FIG. 30. Gametes and incipient gamete union. × 925.

with rather hyaline cytoplasm in which a relatively large central nucleus is embedded.

At least three methods of reproduction occur in *D. globosus*. In actively growing cultures, multiplication is accomplished largely by endogenous cell divisions which produce four new individuals. This process is illustrated in figures 4 and 19 to 23. Figure 4 illustrates a motile cell ready for reproduction. The protoplast has enlarged and almost completely fills the lumen of the lorica. In contrast with certain species of *Haematococcus* (Elliott 1934), *Carteria* (Akins 1941) and *Chlamydomonas* (Bold 1949), in which the flagella disappear at the inception of cell division, those of *D. globosus* persist throughout the process, as in *Brachiomonas* (Hazen 1922), and remain attached to the mother cell lorica long after the daughter protoplasts have been liberated (figs. 19, 20 and 25). The flagella, however, are motionless and become attached to the substratum (cover glass or culture vessel) by their distal extremities (fig. 20). Figures 15 through 18 represent stages of reproduction as observed in stained preparations in which the flagella were not preserved by the techniques employed. While no accurate chromosome counts could be obtained in the material available, the number is in the vicinity of 10 and the divisions of the nucleus are mitotic. Division of the original nucleus is followed by an interphase during which cytokinesis is accomplished by a centrifugal cleavage furrow (fig. 16). This is followed by a second nuclear division (fig. 17) and cleavage (fig. 18), so that four cells are delimited. Centrosomes were not observed in the mitotic figures. As is evident in figures 15 to 18, nuclear and cell division are accompanied by a division of the pyrenoids of the mother cell by elongation and constriction; the newly formed daughter cells, therefore, contain approximately the number of pyrenoids characteristic of the species (fig. 20). Figure 19 represents an individual in which the parent lorica has been ruptured posteriorly by the swelling of the daughter protoplasts which are being liberated. The early stages of liberation are slow, occupying twenty minutes to a half hour from their inception, under the conditions of observation. However, when a certain stage has been reached, the process is completed with a rapidity that almost precludes accurate observation. It is clear, nevertheless, as depicted in figure 20, that the four daughter cells (only three of which are here illustrated for the purpose of clarity) are attached by the proximal portions of their flagella to a hyaline layer of wall material which they have everted as they emerged. The daughter cells remain attached to this hyaline, everted sphere for twenty to thirty minutes; it can be readily observed that only the distal portions of their flagella are beating freely at first. Gradually, the entire flagellum is freed, and when this is accomplished, the individual becomes free swimming. The writers have

observed this process repeatedly and are not aware of a similar one among the unicellular algae.

It should be noted that immediately after their emergence, the daughter cells lack a lorica. However, within twenty minutes after they have emerged a lorica appears (figs. 31, 32); protoplast and lorica increase in size gradually and become separated by a greater distance (figs. 21–23). These young individuals ultimately achieve the size characteristic of the species and then themselves produce four daughter cells.

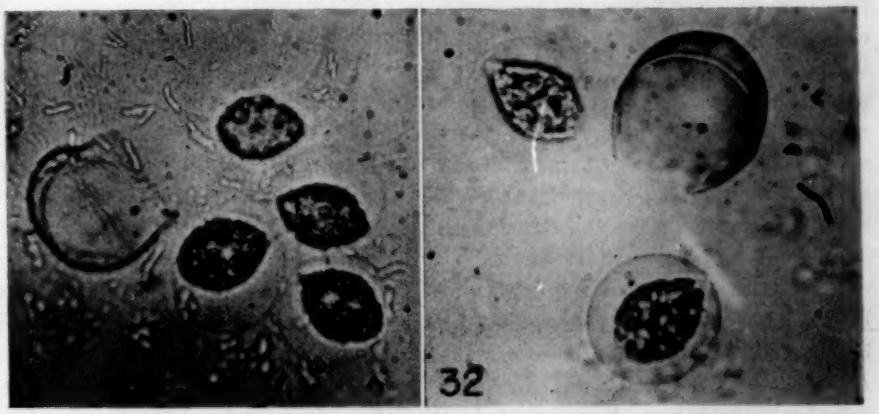


FIG. 31. Photomicrograph of four recently liberated daughter cells and parent lorica; hyaline vesicle of lorica barely visible. × 600. FIG. 32. Photomicrograph of two recently liberated daughter cells and parent lorica. × 600.

In soil-water cultures, after a prolonged period of cell division into motile daughter individuals, a gradual increase in number of cells forming aplanospores becomes evident. This process is illustrated in figures 8–14. One, but more typically four or eight, occasionally, sixteen aplanospores, is formed within one individual. In this process the flagella of the parent cell disappear, perhaps by being retracted into the lorica as illustrated in figure 28. The protoplast then undergoes a series of mitoses and cytokineses. The partitioned segments become walled and remain within the mother lorica for indefinitely long periods unless freed by mechanical pressure (fig. 13). The aplanospores become brownish-red in color because of the deposition of droplets of orange-brown oil, which masks their chlorophyll. That the aplanospores undergo some enlargement during their dormancy, is indicated by the fact that they often partially rupture the mother lorica and some may escape (fig. 14). When transferred to fresh medium, each aplanospore, especially if recently formed, may have its protoplast escape and form a single motile individual (fig. 27).

A third method of reproduction has been observed to occur when aplanospores, which have been stranded on the walls of the culture vessel above the

water level, and thus, somewhat desiccated, are immersed in fresh culture solution. Their behavior is illustrated in figures 29 and 30. Within one and a half to two hours after their immersion in fresh culture solution, each aplanospore of a group may undergo two successive bipartitions forming four protoplasts which develop flagella and become motile. During their development, the lorica of the mother cell, if still intact, is ruptured (fig. 29). The orange-brown daughter protoplasts are now liberated from the aplanospore membrane. When first freed, they are frequently somewhat fusiform, 5.5 to 8.0 microns in length, but they gradually become ovoidal or ellipsoidal. Paired individuals (fig. 30) have been observed frequently and the pairs have remained attached at their anterior poles for periods as long as several hours, but actual union has not been observed in either clonal cultures or mixed cultures. The swarming cells, originating from the germinating aplanospores, often gather in very rapidly moving groups which suggest the clump formation usually associated with sexuality. These minute swarmers have sometimes been observed to develop loricas and grow into small vegetative individuals.

Discussion. Of those biflagellate genera of Phacotaceae in which the loricas are not markedly compressed, only *Dysmorphococcus* is characterized by the possession of two flagellar apertures. The type species of the genus, *D. variabilis*[1] Takeda (Takeda 1916) and the other described species, *D. coccifer* Korschikov (Korschikov 1925) differ in a number of respects from *D. globosus*. The latter may be distinguished by its somewhat larger size (up to 28 microns as compared with 19 microns in *D. variabilis* and 22 microns in *D. coccifer*), the presence of a prominent lorica papilla, globose form, doubly attenuated protoplast, the unpored lorica, the formation of more than one aplanospore and especially by the method of liberation of the daughter individuals. The attributes of the three species are summarized in tabular form in Table 1.

Although the mechanism of liberation of daughter cells is so unusual in *D. globosus*, the writers are of the opinion that it is insufficient to warrant removal of the plant into a different genus. *D. coccifer* and *D. globosus* agree in many respects as to the structure of their protoplasts. However, in addition to difference in method of dehiscence, *D. coccifer* lacks a lorica papilla, an attribute which such a competent microscopist as Korschikov would certainly not have overlooked. The three species of *Dysmorphococcus* may be readily identified by means of the following key:

A. Lorica with hemisphaerical papilla ..... *D. globosus*
A. Lorica lacking prominent papilla ..... B.
B. Protoplast with one pyrenoid ..... *D. variabilis*
B. Protoplast with many pyrenoids ..... *D. coccifer*

[1] Pascher (1927) erroneously refers to this species as *D. Fritschii*.

TABLE 1 *Comparison of attributes of three species of Dysmorphococcus*

Attribute	*D. variabilis*	*D. coccifer*	*D. globosus*
I. LORICA			
a. shape	irregular-globose	flattened-globose	globose, not flattened
b. size	up to 19μ × 17μ × 14μ	up to 22μ	up to 28μ
c. ornamentation	pored	pored	mosaic-punctate
d. papilla	rudimentary, beak-like	absent	present, hemisphaerical
e. dehiscence	longitudinal, 2 valves	longitudinal, 2 valves	posterior, irregular
II. PROTOPLAST			
a. shape	pyriform	globose	bi-attenuate
b. pyrenoids	one, basal	many, peripheral	many, peripheral
c. contractile vacuoles	two, apical	many, peripheral	many, peripheral
d. stigma	discoidal, equatorial to anterior	hemisphaerical, equatorial	linear, equatorial
III. WALL	absent	present	absent
IV. REPRODUCTION			
a. zoospores	2 motile daughter cells	unknown	4 motile daughter cells
b. aplanospores	unknown	one aplanospore (akinete) per mother cell	one to sixteen aplanospores per mother cell
c. germination of aplanospores	not observed	4 zoospores	4 zoospores-facultative gametes?

SUMMARY

1. A new species of *Dysmorphococcus, D. globosus,* is described, based on material collected in rock pools of the old bed of the Caney Fork River, Rock Island, Warren County, Tennessee.

2. The organism has been maintained in uni-algal condition in soil-water cultures and has been studied in the living condition and in fixed and stained preparations.

3. Asexual reproduction is accomplished by division of the parent protoplast within the lorica into four daughter cells, which are liberated in the motile condition; during this process the flagella of the original cell persist, their distal extremities being attached to the substratum. Liberation of the daughter cells is through a posterior rupture of the parent lorica, accompanied by an eversion of a hyaline vesicle.

4. In cultures in which the nutrient supply is being exhausted, each individual may divide internally to form, typically, eight aplanospores. These may germinate directly, each forming one new vegetative cell, or,

after desiccation, each aplanospore may germinate into four minute swarmers which give indications of gamete nature, although zygote formation has not been obtained.

5. Herbarium specimens of this organism have been deposited in the herbarium at Vanderbilt University and at the Chicago Museum of Natural History. Cultures of the organism are maintained at Vanderbilt University and at Indiana University.

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AFFINITIES OF THE GRASS GENUS BECKMANNIA HOST[1]

JOHN R. REEDER

The genus *Beckmannia* comprises two species: *B. eruciformis* (L.) Host, a native of Europe, and *B. syzigachne* (Steud.) Fern., which occurs in North America and temperate Asia. The first of these species, the type of the genus, was originally described as *Phalaris eruciformis* by Linnaeus in his Species Plantarum. It was recognized as a distinct genus by Host some 50 years later and the name *Beckmannia*, in honor of the botanist Johann Beckmann, was published in 1805. The second species was originally described as *Panicum syzigachne* by Steudel in 1846, and it was not until 1928 that this species was transferred, by Fernald, to its proper place in the genus *Beckmannia*.

Not only were these two species originally described as members of two distantly related genera, but the relationship of *Beckmannia* to other genera of Gramineae seems not to have been readily apparent. We find that Steudel (1855), although recognizing the genus as distinct from *Phalaris*, included it in the tribe Phalarideae. Bentham and Hooker (1883), on the other hand, treated it as a member of the Paniceae. Hackel (1887) was apparently the first author to include *Beckmannia* in the tribe Chlorideae and most subsequent agrostologists have followed his placement of this interesting genus.

According to Hitchcock (1950) the only character which the genera of the Chlorideae have in common, aside from the characters which place them in the subfamily Festucoideae, is the arrangement of the spikelets in one-sided spikes. As far as gross morphology is concerned, this indeed seems to be the case. Although the inflorescence of *Beckmannia* is a panicle, the spikelets have very short pedicels and are arranged on only one side of the panicle branches. These spikelets, to be sure, fall with the glumes attached, whereas in most members of the Chlorideae the spikelets disarticulate above the glumes and (when several flowered) between the florets. These differences, however, would not exclude *Beckmannia* from the Chlorideae since there are other members of the tribe in which the spikelets disarticulate below the glumes and in certain species several spikelets may fall attached to a short branchlet. Moreover, the panicle branches of *Beckmannia* might be interpreted as one-sided spikes since, as stated above, the short pedicelled spikelets are borne on only one side of the axis.

[1] This research was supported in part by a grant from the National Science Foundation.

It has long been recognized that the genera of Gramineae may be rather readily classified into two great groups or subfamilies. Robert Brown (1814) was apparently the first author to record the observation that in one group (the Panicoideae) there is a tendency for aborted flowers to be borne at the base of the spikelet, while in the other (the Festucoideae)[2] aborted or rudimentary flowers are borne above the fertile ones. Bentham (1882), who credits the discovery to Munro, has noted further that in the Panicoideae the disarticulation of the spikelet is usually below the glumes, while in the Festucoideae the spikelets break above the glumes and between the florets. It is usually true also that the spikelets are dorsally compressed in the genera of Panicoideae and laterally compressed in Festucoideae. Using these criteria, the tribe Chlorideae must be placed with the Festucoideae since (1) the aborted flowers are borne above the fertile ones, (2) the spikelets are laterally compressed, and (3) in most members the spikelets disarticulate above the glumes.

Members of the two subfamilies differ not only in gross morphological features but also in chromosome size and number (Avdulov 1931), in leaf anatomy (Prat 1936), and in the structure of embryos and seedlings (Van Tieghem 1897). When these other criteria are applied, a slight realignment of the tribes is indicated, but on the whole the composition of the subfamilies

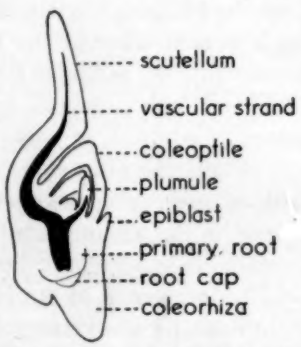

FIG. 1. Median sagittal section of the embryo of *Beckmannia syzigachne* showing the parts.

remains much the same. In fact, Van Tieghem, who arranged the tribes into subfamilies on the basis of embryos and seedlings, remarks that the similarity of his classification to that of Bentham, who used gross morphology only, is: "remarquable si l'on réfléchit à la profonde différence de nature des caractères invoqués."

The value of the study of grass embryos as a possible aid in classification has been recognized not only by Van Tieghem but also by several other

[2] Students of the Gramineae are not in agreement as to the appropriate names for these taxa. Names used in this paper follow Hitchcock (1950).

workers, among them Bruns (1892) and Kennedy (1899). Since a rather specialized terminology is used in referring to the parts of these interesting embryos, a brief explanation follows. As seem in median sagittal section (fig. 1), the single cotyledon (scutellum) is a prominent lateral organ the tip of which extends above the coleoptile. On the opposite side, and inserted at about the same level as the scutellar trace, there may be a small organ

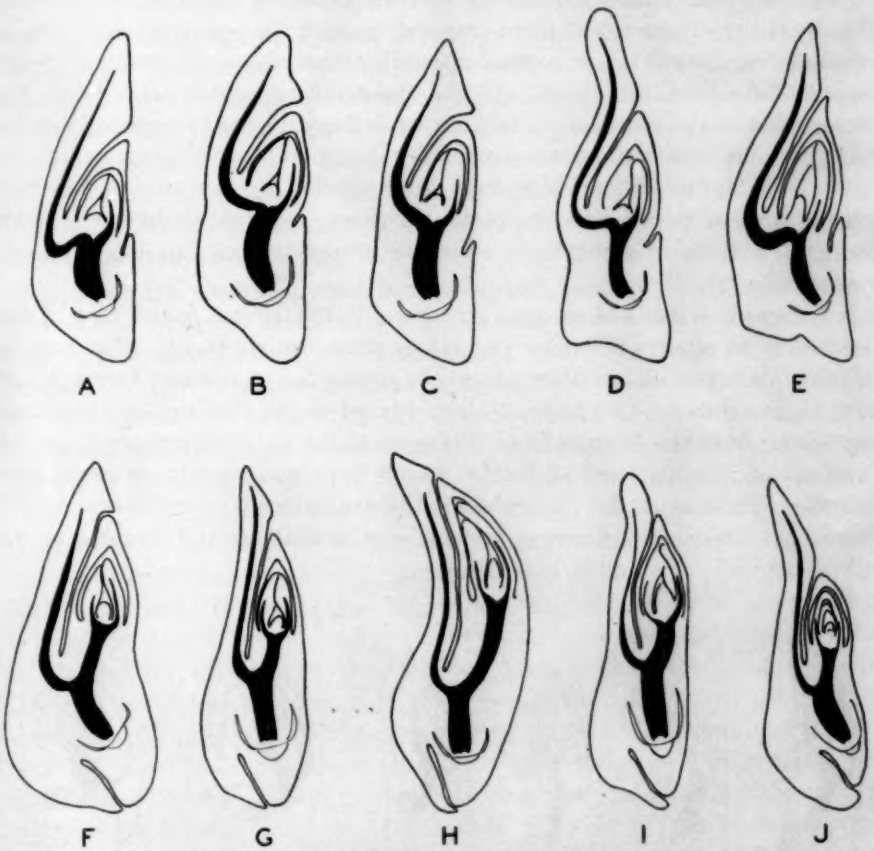

FIG. 2. Median sagittal sections of embryos of species representing various genera and tribes of Gramineae. A, *Festuca elatior* (Festuceae); B, *Dactylis glomerata* (Festuceae); C, *Deschampsia flexuosa* (Aveneae); D, *Phalaris arundinacea* (Phalarideae); E, *Phleum alpinum* (Agrostideae); F, *Panicum clandestinum* (Paniceae); G, *Brachiaria platyphylla* (Paniceae); H, *Echinochloa crusgalli* (Paniceae); I, *Setaria italica* (Paniceae); J, *Sorghum vulgare* (Andropogoneae). A–E, subfamily Festucoideae. Note absence of prominent cleft between lower part of scutellum and coleorhiza and also that the point of divergence of the scutellum bundle is directly below the coleoptile. F–J, subfamily Panicoideae. Note the prominent cleft between the lower part of the scutellum and the coleorhiza and also the distinct elongation between the point of divergence of the scutellum bundle and the coleoptile. These drawings were made with the aid of a microprojection drawing apparatus and are not all to the same scale.

(epiblast) which some authors have considered to be a reduced cotyledon. The primary root is enclosed in a sheath (coleorhiza). The plumule is also enclosed in a sheath (coleoptile) which typically has two vascular bundles, one on either side.[3] Vascular tissue may be seen extending through the root into the shoot with a side branch to the scutellum. Neither the coleorhiza nor the epiblast develops vascular tissue.

Van Tieghem distinguished two basic types of embryos within the family. In the Panicoideae the descending part of the scutellum is free from the coleorhiza, and the coleoptile is inserted well above the point of divergence of the scutellum bundle. In the Festucoideae, on the other hand, the lower part of the scutellum is lacking, or is fused to the coleorhiza, and the coleoptile is inserted at approximately the point of divergence of the scutellum bundle. These facts have been verified by the studies reported in the present paper, and the basic differences may be readily seen when sagittal sections of embryos of members of the two subfamilies are compared (fig. 2).

Using his criteria of embryo structure, Van Tieghem found that it was necessary to remove the tribe Chlorideae from the subfamily Festucoideae and to place it with the Panicoideae. Likewise the two tribes, Oryzeae and Tristigineae, which had formerly been placed in the Panicoideae, appeared to belong with the Festucoideae. These were the only differences from the systems of Bentham and of Hackel which were based solely on gross morphology. The case of the Chlorideae is the one with which we are concerned here. By referring to figure 3, it will be seen that sagittal sections of the

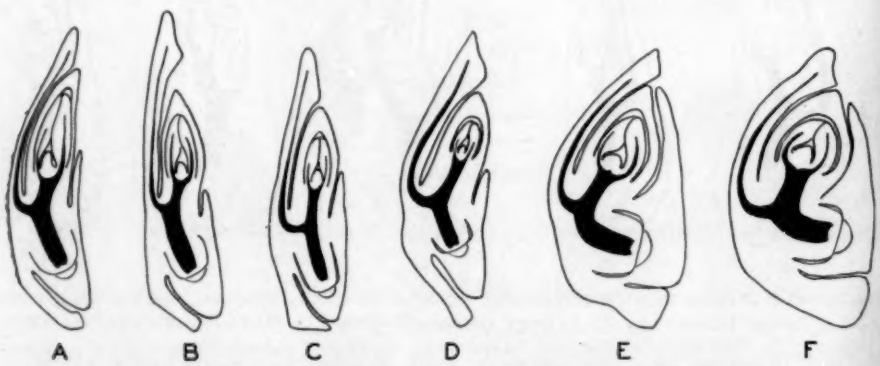

FIG. 3. Median sagittal sections of embryos representing various genera of the tribe Chlorideae. A, *Chloris verticillata;* B, *Schedonnardus paniculatus;* C, *Buchloë dactyloides;* D, *Leptochloa scabra;* E, *Dactyloctenium aegypticum;* F, *Eleusine indica.* Note the similarity of these embryos to those of the tribe Paniceae, (fig. 2, F–I). The most obvious difference is the presence of an epiblast in genera of Chlorideae. These drawings were made in the same manner as described for those in fig. 2.

[3] These bundles are not evident in sagittal section, but are readily seen in a transverse section of the coleoptile or in a longitudinal face section.

embryos of species representing various genera of Chlorideae show a striking resemblance to those of *Panicum* and related genera. In both groups the embryos show the prominent cleft between the lower part of the scutellum and the coleorhiza, as well as a distinct elongation between the point of divergence of the scutellum bundle and the coleoptile. The most obvious difference appears to be the presence of a more or less well-developed epiblast in embryos of members of the tribe Chlorideae. The presence or absence of an epiblast is, in itself, probably of little significance. Some members of the Festuceae have evident epiblasts while others have none. The same condition can be seen in the Hordeae (Kennedy 1899). If the embryos of Chlorideae (fig. 3) are compared with those of typical genera of Festucoideae and Panicoideae (fig. 2), it is readily apparent that they are quite different from those of the former, while strikingly similar to those of the latter.

Other lines of evidence also indicate that the affinities of genera of the tribe Chlorideae are with the Panicoideae rather than with the Festucoideae where they are placed by most agrostologists. Avdulov (1931) and others have found, for example, that the basic chromosome number in most Festucoideae is 7 and that the chromosomes are relatively large. In the Panicoideae, on the other hand, there is a different basic number and the chromosomes tend to be small. In the Chlorideae, in general, the chromosomes are small and the basic number is 5, 6 or 9; in other words, they are like those of the Panicoideae.

Prat (1936), who has studied the histology of the leaf and sheath epidermis of Gramineae, finds that there are two general types—a panicoid and a festucoid. It seems highly significant that in the tribe Chlorideae the leaf structure is of the panicoid type. In his comprehensive paper, Prat reviews the evidence from various lines of research, and there seems little doubt that the affinities of the Chlorideae are with members of the subfamily Panicoideae and not with the Festucoideae. The investigations reported in the present paper certainly support this view. Stebbins (1950) states that in the highly important grass family the present evidence indicates that histological and cytological characteristics provide more certain clues to the true affinities of genera than do those of the gross external morphology of the inflorescence (including spikelets and flowering scales), which are the basis for the traditional systems of classification of the family. Systematic agrostologists have, however, continued to base their classifications principally upon gross morphological similarities, and have largely ignored important histological and cytological data.

While the evidence from several different lines of research supports the view that the Chlorideae must be considered as members of the subfamily Panicoideae, the genus *Beckmannia* presents a problem. A sagittal section of the embryo of *B. syzigachne* shows it to be of the festucoid type (fig. 4, d).

On checking the literature, I find that Van Tieghem (1897), who worked with *B. eruciformis,* also made this same observation and remarked that *Beckmannia* should be removed from the Chlorideae. Two other authors, however, who studied and figured embryos of numerous grasses apparently failed to note that the embryo of *Beckmannia* differed from those of members of the Chlorideae. Bruns (1892) lists *Beckmannia* with the Chlorideae but he shows no figure nor does he mention this genus in his discussion. Kennedy (1899) states that according to the characteristics of their embryos, the Chlorideae are more closely allied to the Andropogoneae (subfamily Pani-

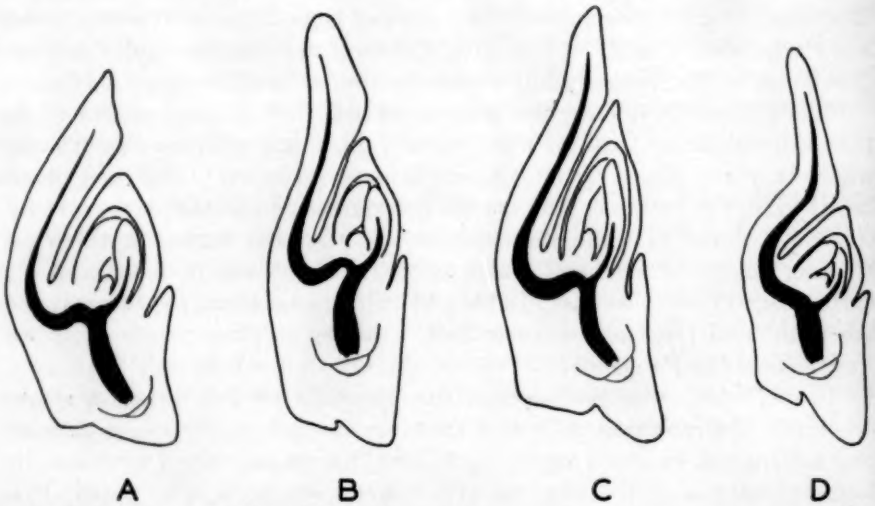

FIG. 4. Median sagittal sections of the embryos of *Beckmannia* and three genera of the tribe Agrostideae. A, *Polypogon monspeliensis;* B, *Alopecurus geniculatus;* C, *Phleum alpinum;* D, *Beckmannia syzigachne.* Note the striking similarities of these embryos. All are quite obviously of the festucoid type and all have a small epiblast and a slight cleft between the lower part of the scutellum and the coleorhiza. The embryo of *Beckmannia* is seen to be quite different from those of the genera of Chlorideae (fig. 3). Drawings prepared in the manner described for figures 2 and 3.

coideae) than to the Aveneae and Festuceae (subfamily Festucoideae). He described the embryos of several genera of Chlorideae indicating that the divergence of the scutellum bundle is some distance below the base of the plumule and that there is a cleft between the scutellum and coleorhiza. He states that in *Eleusine coracana* the scutellum bundle is inserted close to the base of the plumule, but this is incorrect. I have sectioned embryos of this species and find that the distance between the insertion of the scutellum bundle and the plumule is quite as great as it is in *E. indica* (fig. 3, f). Kennedy also states that the embryo of *Beckmannia* has about the same characteristics as those of other Chlorideae, and he presents a figure which

would seem to bear this out. The drawing is incorrect, however, as he shows the scutellum bundle inserted at some distance below the plumule, while it is actually directly below as shown in my figure 4, d.

As stated above, the evidence from embryo studies strongly indicates that *Beckmannia* is incorrectly placed with the tribe Chlorideae. There are, moreover, other lines of evidence which support this same conclusion. Prat has pointed out that the epidermis and leaf anatomy of this genus is of the festucoid type, while the Chlorideae, on the whole, show distinct panicoid characteristics. Furthermore, *Beckmannia* has a chromosome number of $14(x=7)$[4], which is quite different from that of genera of Chlorideae as previously mentioned.

The evidence from cytology, anatomy, and embryo studies thus is in complete agreement that *Beckmannia* is not closely related to other genera of Chlorideae. Various authors (Van Tieghem 1897, Avdulov 1931, Prat 1936, Krishnaswamy 1941) have pointed out that *Beckmannia* should be removed from the Chlorideae, and Avdulov and Prat have suggested that it be placed in the tribe Festuceae. The work reported in the present paper, supported by evidence from other lines of research, indicates that *Beckmannia* has stronger affinities with genera of the tribe Agrostideae. Figure 4 shows a sagittal section of the embryo of *Beckmannia* along with those of *Alopecurus, Phleum,* and *Polypogon.* Striking similarities among the embryos of these four genera are at once apparent. All lack an elongation between the point of divergence of the scutellum bundle and the coleoptile, all have a small epiblast, and there is a very slight cleft at the base of the scutellum between that organ and the coleorhiza. The characteristics of the epidermis and leaf anatomy are also similar in members of these genera (Prat 1936). Another salient point is that the basic chromosome number in these genera of Agrostideae is 7 (Avdulov 1931), which is also the number in *Beckmannia.* The chromosomes, moreover, have a similar morphology. It may also be significant that, as reported by Martin (1946), the endosperm in the seed of *Beckmannia* is soft-fleshy in consistency and it is thus similar to that found in *Alopecurus* and *Cinna,* both of which are members of the tribe Agrostideae. Similar endosperm is also present in the seeds of certain members of the Aveneae.

The structure of the embryo of *Beckmannia,* therefore, indicates strongly that the genus is allied to genera of the tribe Agrostideae, and this evidence finds support on cytological and anatomical grounds. In view of the above, it seemed desirable to compare, on the basis of traditional gross morphological characters, the genera concerned. The most diagnostic characteristic for

[4] Dr. Norman H. Giles, Jr., has counted the chromosomes in root tips of my *Beckmannia* material and finds that the number is 14. This count is in agreement with those of other workers.

the tribe Agrostideae is the presence of 1-flowered spikelets. *Beckmannia* might cause some concern on this point, since although in *B. syzigachne* the spikelet bears only a single floret, in *B. eruciformis* 2-flowered spikelets occur. Occasionally members of the classical Agrostideae bear 2-flowered spikelets, however, so this in itself would not appear to be sufficient grounds to exclude *Beckmannia* from the tribe. In the Agrostideae the inflorescence may be an open, contracted, or spike-like panicle, but never a true spike. The inflorescence of *Beckmannia* is a panicle, the spikelets being borne on short pedicels along the ultimate branches. The members of the tribe Agrostideae with which I have chosen to compare *Beckmannia* in this paper (*Phleum*, *Alopecurus*, and *Polypogon*) all share with that genus the characteristic of having spikelets which fall as a unit, the disarticulation being below the glumes. The glumes of all are keeled and large, covering the floret within. The inflorescence is a contracted panicle, which is more or less spikelike in appearance. In the panicle of *Beckmannia*, the branches are more or less appressed to the rachis, except at anthesis, and if they were partially fused, the structure would be quite similar to the inflorescence of *Phleum*. Thus *Beckmannia* would seem to fit rather readily into the Agrostideae on the basis of its gross morphology, as well as on the other criteria cited. The evidence for the removal of the genus *Beckmannia* from the tribe Chlorideae appears to be overwhelming. The similarity of this genus to members of the Chlorideae rests solely upon superficial morphological grounds. If, on the other hand, *Beckmannia* is considered to be a member of the Agrostideae, such an arrangement appears to be a natural one, and is supported by many different lines of evidence.

List of species discussed and sources of material. The embryos figured in this paper were secured from mature seeds which were either collected in the field or were taken from herbarium sheets. These were embedded in paraffin, sectioned at 10 microns, and stained with saffranin and fast green. Unless otherwise indicated, specimens are deposited in the Herbarium of Yale University.

Alopecurus geniculatus L.

Newfoundland: *E. H. Eames & C. C. Godfrey*, July 23, 1908.

Beckmannia syzigachne (Steud.) Fernald

Oregon: *J. R. Reeder & C. G. Reeder 1857.*

Brachiaria platyphylla (Griseb.) Nash

Mexico: state of Chihuahua, *J. R. Reeder, C. G. Reeder & L. N. Goodding 1685.*

Buchloë dactyloides (Nutt.) Engelm.

Colorado: *Crandall 592.*

Chloris verticillata Nutt.
Texas: *F. Tweedy*, May 1880.
Dactylis glomerata L.
Massachusetts: seeds collected on grounds of Arnold Arboretum.
Dactyloctenium aegypticum (L). Beauv.
North Carolina: *H. L. Blomquist 9827* (Herb. Gray).
Deschampsia flexuosa (L.) Trin.
New Hampshire: *J. R. Reeder 911.*
Echinochloa crusgalli (L.) Beauv.
Iowa: *J. R. Reeder & C. G. Reeder 1701.*
Eleusine indica (L.) Gaertn.
Massachusetts: *J. R. Reeder & C. G. Reeder 259.*
Festuca elatior L.
Massachusetts: seeds collected on grounds of Arnold Arboretum.
Leptochloa scabra Nees
New Guinea: *Brass 3725* (Herb. Gray).
Panicum clandestinum L.
Massachusetts: *J. R. Reeder & C. G. Reeder 240.*
Phalaris arundinacea L.
Massachusetts: seeds collected near historic Concord Bridge.
Phleum alpinum L.
Oregon: *Elihu Hall 610.*
Polypogon monspeliensis (L.) Desf.
Oregon: *Elihu Hall 624.*
Schedonnardus paniculatus (Nutt.) Trel.
Colorado: *C. S. Crandall 633.*
Setaria italica (L.) Beauv.
Harvard Univ. Econ. Bot. Coll. No. 5576.
Sorghum vulgare Pers.
Harvard Univ. Econ. Bot. Coll. No. 5575.

SUMMARY

1. Histological investigations of grass embryos presented here lend support to previous suggestions: that the tribe Chlorideae should be removed from the subfamily Festucoideae and placed with the Panicoideae and that *Beckmannia* is not closely related to genera of the Chlorideae, even though it has long been treated as a member of that tribe.

2. It is here proposed that a more natural arrangement is achieved by placing *Beckmannia* in the tribe Agrostideae, since it seems to have close affinities with such genera as *Phleum*, *Alopecurus*, and *Polypogon*.

3. Previous histological and cytological studies tend to support this suggestion. Even on the basis of its gross morphological characters *Beck-*

mannia appears to be more closely allied to members of the Agrostideae, and especially to those mentioned above, than to genera of the Chlorideae.

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BIOCHEMICAL INVESTIGATIONS IN SACCHAROMYCES

M. AHMAD

Biochemical investigations in micro-organisms have helped in tracing the paths of syntheses of many essential biological substances in microbiological assay. Interesting studies on the ability of yeasts to synthesize various members of Vitamin B complex and amino acids have been carried out by Burkholder (1943), Burkholder and Moyer (1943), Burkholder, McVeigh and Moyer (1944) and McVeigh and Bell (1951). Lindegren (1949) has not only brought to light the nutritional requirements of some yeast but has also studied the mechanism of inheritance of factors controlling the syntheses of the nutrilites.

The present paper constitutes a report on the nutritional requirements of 11 strains of *Saccharomyces*. It further incorporates genetical studies on two of these yeasts, *S. cerevisiae* and *S. carlsbergensis*.

Material and methods. Investigations were carried out on the following yeasts: Danish Baking Yeast *(Saccharomyces cerevisiae)* from Distillers Company Limited, Surrey; *S. cerevisiae* Hansen 381, *S. cerevisiae* Hansen 815, and *S. cerevisiae* 2160 from the National Collection of Type Culture, London; *S. cerevisiae* from Delft, Holland; *S. cerevisiae* or *ellipsoideus* (Baker's Yeast), *S. cerevisiae* (Brewer's Yeast), *S. carlsbergensis* and *S. carlsbergensis*, Fleischmann 4228 from Professor Hopkins, University of Birmingham; *S. carlsbergensis* from Delft, Holland and *Saccharomyces sp.* Form 237, from Professor Winge, Copenhagen.

Of the above yeasts, Danish Baking Yeast *(Saccharomyces cerevisiae)*, *S. cerevisiae* or *ellipsoideus* (Baker's Yeast), and *S. cerevisiae* (Brewer's Yeast) were acquired through the kindness of Dr. M. Ingram of the Low Temperature Research Station, Cambridge, and *Saccharomyces sp.* Form 237 through Dr. R. Davies of the Department of Biochemistry, Cambridge.

A synthetic medium was made after Burkholder (1943) and Burkholder, McVeigh and Moyer (1944) with the following composition per litre: Dextrose, 20 gm.; recrystallized asparagine, 2 gm.; $MgSO_4 \cdot 7H_2O$, 0.5 gm.; $CaCl_2 \cdot 2H_2O$, 0.33 gm.; $(NH_4)_2\ SO_4$, 2.0 gm.; Kl, 0.1 mg. Trace elements were added to this medium in parts per million as follows: B, 0.01; Mn, 0.01; Zn, 0.07, Cu, 0.01; Mo, 0.01; and Fe, 0.05. Sodium borate, manganese chloride, Zinc sulphate, copper sulphate, sodium molybdate and ferrous sulphate were the actual forms in which these trace elements were used.

Vitamin supplements were added in gamma per litre of medium as follows: thiamine, 200; riboflavin, 100; pyridoxine, 200; niacin, 200;

biotin, 2; pantothenic acid, 200; and inositol, 1000. Thiamine hydrochloride, pyridoxine hydrochloride, biotin methyl ester, and calcium pantothenate were the actual forms of these vitamin compounds used.

Nine kinds of media were prepared for testing the vitamin requirements of each yeast as follows: one with no addition of vitamins, another with the addition of all the seven vitamins, and seven with single omissions of each of the seven vitamins.

The reaction of each solution was adjusted to pH 5 and all were poured in $6 \times 3/4''$ tubes. Uniformity of tubes was maintained to avoid any effects due to shapes and sizes of vessel (Clark 1922, Miller Eastcott & Maconachie 1933). The media were then sterilized at 15 pounds pressure for 15 minutes.

Since the behavior of old cultures differ (Leonian & Lilly 1942, Knight 1945) each stock was subcultured for 48 hours in 2% malt and after draining the liquid a loopful of it was inoculated in a tube containing 5 cc. of the basal synthetic medium. The loop had an inside diameter of 4 mm. In order to wash off all trace of malt from the surface of the cells the tube was well shaken. Next, by means of the previous loop, one loopful of this suspension of yeasts was transferred to each of the 9 kinds of tubes. The cultures were then incubated for 72 hours at 25°C after which observations on growth were made.

Results. The data from the 11 yeasts have been summarized in table 1. A positive sign has been put where there was sufficient growth and a negative sign where there was no growth. By the latter it is, however, not meant that in these cases there was no increase over the amount of the inoculum but that the medium remained completely clear to the naked eye. E.L. in the table stands for extremely little growth and V.L. for very little growth. Both these have been taken as equivalent to no growth. L. stands for little growth and has been taken as evidence for sub-optimal synthesis, of the vitamin in question, but the culture classed as synthesiser.

As seen from the table of the 11 yeasts tested, one *S. cerevisiae,* Brewer's Yeast, proved to be completely autotrophic while another, *S. cerevisiae* 2160, possessed the capacity of synthesising all the seven vitamins when one of them were missing at a time but failed to grow when all of them were absent from the synthetic medium. Of the nine heterotrophic ones, seven proved to be poor or very poor synthesisers of biotin, seven of them also showed pantothenic acid deficiency. Two showed deficiency in pyridoxine synthesis and one in thiamine.

Grouping the strains into species one finds that of the five heterotrophic strains of *S. cerevisiae* four were deficient and a fifth suboptimal for biotin synthesis. The same was true for their capacities to synthesise pantothenic acid. Of the three strains of *S. carlsbergensis* two lacked the capacity to

synthesise pyridoxine and the third was sub-optimal for it.

Dominance in vitamin syntheses. In order to study dominance with respect to vitamin B group syntheses two heterothallic Yeasts, *S. cerevisiae* Danish Baking Yeast and *S. carlsbergensis* Delft were selected. As will be seen from table 1, the former synthesised pyridoxine but failed to synthesise

TABLE 1. *Showing vitamin requirement of 11 strains of Saccharomyces species.*

No.	Designation of strain	Growth in synthetic media								
		No vitamins.	No thiamine.	No riboflavin.	No biotin.	No niacin.	No inositol.	No pyridoxine.	No pantothenic acid	+ All vitamins.
1.	*S. cerevisiae*, Danish Baking Yeast.	–	+	+	V.L.	+	+	+	–	+
2.	*S. cerevisiae*, Hansen 381.	–	+	+	L	+	+	+	–	+
3.	*S. cerevisiae*, Hansen, 815.	–	+	+	V.L.	+	+	+	L	+
4.	*S. cerevisiae*, Hansen, 2160.	–	+	+	+	+	+	+	+	+
5.	*S. cerevisiae*, Delft.	–	+	+	V.L.	+	+	+	–	+
6.	*S. cerevisiae* or *ellipsoideus*, Baker's Yeast.	–	+	+	E.L.	+	+	+	–	+
7.	*S. cerevisiae*, Brewer's Yeast.	+	+	+	+	+	+	+	+	+
8.	*S. carlsbergensis*.	–	+	+	V.L.	+	+	–	+	+
9.	*S. carlsbergensis*, 4228.	–	+	+	+	+	+	L	V.L.	+
10.	*S. carlsbergensis*, Delft.	–	+	+	+	+	+	–	–	+
11.	Form 237	–	+	+	E.L.	+	+	+	–	+

pantothenic acid while the latter synthesised both pyridoxine and pantothenic acid.

The Danish Baking Yeast formed four spored asci and five such asci were dissected and four spores from each of them grown separately. Out

TABLE 2. *Showing heterothallic nature of Danish Baking yeast, S. cerevisiae and its homozygosity for the various genes controlling vitamin syntheses.*

The four single spore progenies from ascus 3.	Mating reaction	Growth in synthetic media								
		No Vitamins	No thiamine	No riboflavin	No biotin	No niacin	No inositol	No pyridoxine	No pantothenic acid	+ All Vitamins
A	(+)	+	+	+	V.L.	+	+	+	–	+
B	(+)	+	+	+	V.L.	+	+	+	–	+
C	(–)	+	+	+	L	+	+	+	–	+
D	(–)	+	+	+	V.L.	+	+	+	–	+

of the five asci dissected, four spores from only one of them, ascus 3, gave viable progenies. These single spore progenies were designated A, B, C, and D arbitrarily and were tested for mating reaction and vitamin synthesis.

As seen from table 2, progenies from spores A and B proved to be (+) and from spores C and D (−). With regard to vitamin synthesis all the four single spore cultures from the ascus showed the same requirements as the diploid parent. Danish Baking Yeast was thus found to be homozygous for the dominant as well as recessive genes involved in vitamin syntheses.

S. carlsbergensis from Delft formed only two spored asci, and of the first few single spore progenies tested some showed lack of growth even in media with all the seven vitamins. When these segregants, which failed to grow in an all vitamin medium, were tested for amino-acid deficiency, they were found to need methionine. Methionine was therefore included as one of the nutrilites.

Seventy-five asci were dissected to study segregations for the synthesis of methionine and the various members of vitamin B group. Only in the case of 7 asci did both the spores give progenies and the data from these fourteen single spore cultures are summarized in table 3.

TABLE 3. *Showing mating type segregation and growth factor requirements in single spore cultures from seven asci of S. carlsbergensis from Delft.*

No of Ascus	Designation of culture	Mating reaction	Growth in synthetic media									
			No Vitamins	No Thiamine	No riboflavin	No biotin	No niacin	No inositol	No pyridoxine	No pantothenic acid	No methionine	+ All Vitamins + Methionine
13	a	(−)	−	+	+	+	+	+	−	−	−	+
	b	(+)	−	+	+	+	+	+	−	−	+	+
22	a	(+)	−	+	+	+	+	+	−	E.L.	−	+
	b	(−)	−	+	+	+	+	E.L.	−	−	+	+
24	a	None	−	+	+	+	+	+	−	−	−	+
	b	None	−	+	+	V.L.	+	+	−	−	+	+
25	a	(−)	−	+	+	V.L.	+	+	−	−	+	+
	b	(+)	−	+	+	+	+	+	−	−	−	+
28	a	None	−	+	+	+	+	+	E.L.	+	+	+
	b	None	−	+	+	+	+	+	−	−	−	+
47	a	(+)	−	+	+	+	+	+	−	−	+	+
	b	(−)	−	+	+	+	+	+	E.L.	E.L.	−	+
8	a	(+)	−	+	+	+	+	+	−	E.L.	−	+
	b	(−)	−	+	+	+	+	+	−	+	+	+

In five asci out of seven, one spore proved to be (+) and the other (−) while in the remaining two asci both the spores failed to give any mating reaction. With regard to the synthesis of methionine in all the seven asci

one spore proved to be a synthesiser and the other a non-synthesiser. *S. carlsbergensis* Delft is therefore heterozygous for the methionine synthesis genes and synthesis of methionine is dominant to its non-synthesis. It is further seen that the failure of some single spore cultures to give a mating reaction does not interfere with the regularity of segregation of the methionine alleles. Thus in asci 24 and 28 although both segregants fail to give a mating reaction yet they are normal segregants for the methionine locus.

All the fourteen spores possessed the capacity of synthesising thiamine, riboflavin and niacin like the parent. One spore showed extremely little capacity to synthesise inositol and two spores showed a sub-optimal synthesis of biotin unlike the parent. All except two spores lacked the capacity to synthesise pyridoxine. Synthesis in these two exceptional cultures was only sub-optimal. Two spores surprisingly showed the capacity of synthesising pantothenic acid which the "diploid" parent lacked.

Hybrid between Danish Baking Yeast, S. cerevisiae and S. carlsbergensis. A hybrid was made by crossing the haplophase, 3c, from Danish Baking Yeast [(−), and pantothenicless] with the haplophase 13b from *S. carlsbergensis* Delft [(+), pyridoxineless, and pantothenicless]. The hybrid synthesised not only pyridoxine but also pantothenic acid (table 4).

TABLE 4. *Showing characters of parents and an interspecific hybrid between S. cerevisiae (Danish Baking Yeast) and S. carlsbergensis, Delft.*

Designation of culture	Mating reaction	Growth in synthetic media								
		No vitamins	No thiamine	No riboflavin	No biotin	No niacin	No inositol	No pyridoxine	No pantothenic acid	+ All Vitamins
Danish Baking Yeast haplophase, 3c	(−)	−	+	+	L	+	+	+	−	+
S. carlsbergensis Delft haplophase, 13b	(+)	−	+	+	+	+	+	−	−	+
Hybrid	None	−	+	+	+	+	+	+	+	+

Synthesis of pyridoxine showed the dominance of the synthesiser allele over non-synthesiser and was in keeping with the expectation but synthesis of pantothenic acid was unexpected for both parents lacked that capacity. This showed that the two parents probably lacked different genes involved in the chain of pantothenic acid synthesis. Another noteworthy feature about the hybrid was that although it synthesised each of the seven members of the vitamin B complex when one of them was missing at a time,

yet it failed to grow in the basal medium where all seven of them were omitted.

Analysis of pantothenic acid synthesis in the Danish baking yeast S. cerevisiae and S. carlsbergensis from Delft. It is considered that a coupling of β-alanine with pantoyl lactone (α-Hydroxy-β, β-dimethyl-γ-butyrolactone) is involved in the biosynthesis of pantothenic acid (Rosenberg 1942, Williams 1943). Organisms may therefore fail to synthesise it for one of several reasons. Some of them may fail to synthesise β-alanine, as is the case with a diphtheria bacillus (Williams 1943) and some yeasts (Nielson and Hartelius 1943, Sarett and Cheldelin 1945). Some may fail to grow due to a block in pantoyl lactone synthesis, as is seen in *Acetobacter* (Underkofler, Bantz and Peterson 1943) and *Clostridium septicum* (Ryan, Ballentine, Stolovy, Corson and Schneider 1945). Still others might fail to synthesise it because they fail to couple β-alanine and pantoyl lactone. The pantothenicless mutant of *Neurospora*, 5531, (Tatum and Beadle 1942) serves as a good example of this class.

β-alanine or pantoyl lactone, or β-alanine and pantoyl lactone were therefore added as supplements to the synthetic pantothenicless medium to determine which of the three alternatives discussed above operated in these two strains of *S. cerevisiae* and *S. carlsbergensis*. Both showed normal growth when supplied with β-alanine but failed to do so when given the pantoyl moiety alone. Hence in both of them the mechanisms of pantoyl lactone synthesis and coupling of β-alanine and pantoyl lactone were intact but the block lay in the synthesis of β-alanine. Since the hybrid between the two strains synthesised β-alanine they probably lack two different genes involved at two different stages in its synthesis.

Discussion. In recent years studies have been made of the capacity of yeasts to synthesise various members of vitamin B complex. None of the yeasts so far investigated are exacting in respect of riboflavin. Most of them have however, proved to be exacting for one or more of the remaining six members of this group of vitamins.

The 11 yeasts investigated are in accord with these findings. None of them was deficient for the synthesis of riboflavin. That strains of *Saccharomyces cerevisiae* were usually deficient for biotin and pantothenic acid was found by Lindegren (1945b & c). Of the three strains of *S. carlsbergensis* investigated, two were non-synthesisers of pyridoxine. The agreement with Lindegren's findings in respect to the vitamin requirements of *S. cerevisiae* and *S. carlsbergensis* suggests that vitamin deficiencies may be of some use in yeast taxonomy when taken in conjunction with fermentation capacities. Yeasts have been classified on the basis of growth factor requirements by Schultz, Atkin and Frey (1940) and Lochhead and Landerkin (1942). They could, however, never be used as a guide

entirely on their own as various strains of the same species differ in their vitamin requirements (Williams 1941) and different species may show the same vitamin deficiencies. For example the strain of *Saccharomyces logos* examined by Burkholder, McViegh and Moyer (1944) was biotin and pantothenic acid deficient as are most strains of *S. cerevisiae* (Table 1 and Lindegren 1945 c)

The findings of Williams (1941), Williams, Eakin and Snell (1940), and Leonian and Lilly (1942) have shown that the presence of one nutrilite may assist in the synthesis of others. Evidence for this was found in *S. cerevisiae* 2160 and in the hybrid between Danish Baking Yeast and *S. carlsbergensis* Delft. Both *S. cerevisiae* 2160 and the hybrid failed to grow in basal synthetic medium lacking all the vitamins but grew perfectly when only one of them was missing at a time. As observed by Williams, Eakin and Snell (1940): "It may be that the one nutrilite by furnishing the means of completing one of several enzyme systems enables the organism to derive energy for metabolic and synthetic activity."

The capacity to synthesise methionine and pyridoxine was dominant to non-synthesis as was found by Lindegren (1945b & c) with respect to pyridoxine, biotin, pantothenic acid and thiamine. It may be recalled that the capacity of various yeasts to ferment diverse carbohydrates has also been found dominant to lack of capacity to do so (Winge and Laustsen 1939b, Lindegren 1945a, Winge and Roberts 1948 and 1950.)

Evidence for β-alanine being involved in the synthesis of pantothenic acid molecule was found in both Danish Baking Yeast and *S. carlsbergensis*, Delft. The two strains, however, appear to lack two different genes controlling the synthesis of β-alanine since their hybrid synthesised β-alanine and thereby pantothenic acid. It is therefore considered that at least two genes are involved in the synthesis of β-alanine. The hypothesis, however, needs genetic confirmation and further biochemical test. The deficiency of these two strains in β-alanine supports the observations of Nielson and Hartelius (1943) and Sarett and Cheldelin (1945) who found that the majority of yeasts deficient in pantothenic acid lack the capacity to synthesise β-alanine.

SUMMARY

Eleven strains of yeasts belonging to the genus *Saccharomyces* were investigated for their vitamin requirements. Two were autotrophic and nine heterotrophic. Most strains of *S. cerevisiae* required biotin and pantothenic acid for growth and strains of *S. carlsbergensis* required pyridoxine. One *S. carlsbergensis* strain was heterozygous for methionine synthesis. Synthesis of methionine and of pyridoxine were found to be dominant over non-synthesis. Two pantothenic acid deficient yeast strains, one being *S. cerevisiae* and the other *S. carlsbergensis*, could not synthesise

β-alanine but the hybrid between the two could do so. It has been concluded therefore that the two strains lack two different genes controlling the synthesis of β-alanine.

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THE DEVELOPMENT OF THE BASIDIUM IN COLEOSPORIUM SIDAE

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Recently the author (1951) described a new species of *Coleosporium* on *Sida*. It is no doubt a heterocious eu-form, but aecia and pycnia are not known. The present paper deals with the morphology, karyogamy and meiosis of the probasidial sorus of *Coleosporium sidae*. Here the term "probasidium" is preferred to the more conventional term "teliospore" because of certain characteristics exhibited by this rust. The "teliospore" in rusts is typically a thick walled structure, each cell of which germinates to produce a basidium. But in *Coleosporium* the so-called "teliospores" are actually thin-walled and they are embedded in a gelatinous matrix. They develop directly into septate basida. Following a suggestion by Olive (1949) the "teliospores" are referred to in this paper as probasidia, while probasidia and basidia are frequently designated together as basidial elements.

The earlier work on the cytology of this genus has been very ably summarised by Olive (1942, 1949). The first complete account of meiosis was given by Holden and Harper (1902) in *C. sonchi-arvensis* and this was followed by Moreau (1914) who described fusion and nuclear divisions in *C. senecionis*. Dodge (1925) later described the morphology and cytology of the probasidial sorus in *Gallowaya pinicola*, a microcyclic species on pine. By far the most detailed and critical account of meiosis has been given by Olive (1942) in *C. helianthi* and this has been followed by the same author (1949) in *C. vernoniae*. In this paper, only those features in the morphology and cytology are given which are of some special interest. Other details have been given by Olive (1949) to whose paper the reader is referred for a more detailed and elaborate account.

Material and methods. The material was collected directly in the field and the leaves were kept in a damp chamber for eight to twelve hours and fixed at various intervals. Only two fixatives were used: formalin-acetic-alcohol and Wilson's modification of the Allen-Bouin's fluid. Both gave excellent results. The usual embedding procedure was followed and the blocks were cut at 4 to 10 μ. The sections were stained with Heidenhain's iron-alum haematoxylin or crystal violet and iodine, of which the latter gave the best results. Fuelgen in combination with light green was also tried but not much success was obtained with this procedure. The figures have been drawn from sections stained with crystal violet, unless otherwise indicated in the legend.

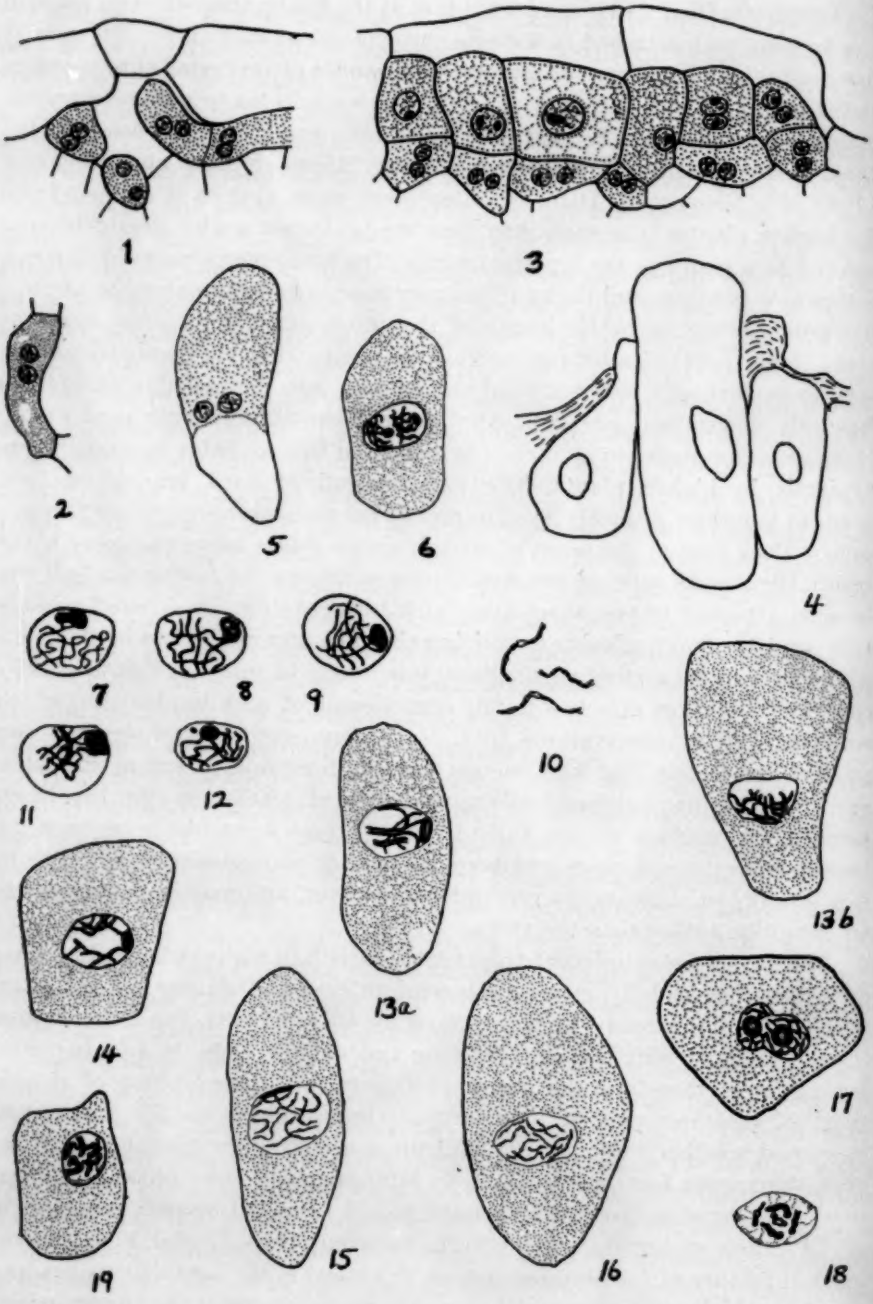
Morphology of the sorus. In a very young infection the hyphae are seen ramifying in the intercellular spaces of the parenchyma cells of the leaf, just below the epidermis. The cells of the hyphae are binucleate (fig. 1). Small branches from these penetrate the host cells in the form of haustoria which are also binucleate. The nuclei in the hyphae are relatively large and each shows a group of chromatin strands with a nucleolus (fig. 2). The hyphae aggregate beneath the epidermis near the seat of the infection and at their tips cut off the binucleate probasidial mother cells (fig. 1). These enlarge rapidly and by conjugate nuclear division and cell division give rise to the probasidial cells which are also binucleate. The probasidial cells enlarge rapidly and the protoplast keeps pace with the development of the probasidium (fig. 3). The two nuclei remain side by side. The probasidial cells secrete apically and laterally some gelatinous substance which gradually increases in quantity as the probasidium approaches maturity (fig. 4). When the sorus is fully mature the epidermis breaks off and the gelatinous matrix, which has by now become continuous over the whole sorus, is exposed to the outside. This serves to protect the probasidial sorus and helps in retaining the moisture for the germination of the basidial elements much as in jelly fungi. The gelatinous matrix takes on a very dark color with crystal violet. There is evidence that the gelatinous substance is secreted in layers, one over another, much as in *Colesporium vernoniae* as described by Olive (1949). In some cases a probasidium rapidly enlarges and pushes through the matrix and is conspicuously exposed to the outside (fig. 4). The significance of such a development is not known.

The writer has not been able to see any trace of catenulations in the sorus. Even up to the time of germination of the basidia only one row of basidial elements can be discerned. But catenulation of the basidial elements has been seen in various other species of *Coleosporium*. Dietel (1903) described it first in *C. vernoniae*, and this has been confirmed by Olive, (1949) who stated that catenulation in various degrees is exhibited by about fourteen species of *Coleosporium* in North America. The probasidial elements sometimes show stalk-like bases (fig. 5). They have also been described in *Gallowaya pinicola* and in *Coleosporium vernoniae*.

Karyogamy. It has been stated above that the probasidial cells are formed as a result of conjugate division in the probasidial mother cells. In a young probasidium the two nuclei lie close together (fig. 3). In each there is a prominent nucleolus and some chromatin material in the form of separate threads closely compacted together. Antecedent to the formation of the fusion nucleus the chromatin threads become loose. The nuclear membranes dissolve at the point of contact of the two nuclei and a continuous membrane is formed. The two sets of chromosomes along with the nucleoli remain distinct for a time, after which they come together (fig. 6).

Prophase. Olive (1949) reported that at the fusion stage the two nucleoli can be seen, each attached to a single chromosome of its own set. The writer has not been able to prove decisively the presence of nucleolar chromosomes, but it is quite likely that they exist, for such nucleolus organizers have recently been reported in several other fungi. McClintock (1945) has reported them for *Neurospora crassa* and Wheeler, Olive, Ernest and Edgerton (1948) for *Glomerella*. There is no leptotene stage such as is characteristic for higher plants. It is suggested that the prefusion nuclei should be considered as already in the leptotene stage. The homologous pairs of chromosomes now synapse, and the synapsis may start either at one end or at various points along the whole length of the chromosome. This is the zygotene stage (figs. 7–14). Under the microscope the pairing chormosomes can be seen to be variously coiled around one another and their double nature can be easily determined (fig. 10). At this stage the chromosomes tend to collapse or accumulate at one place (fig. 11), and this probably corresponds to synizesis in higher plants. The two nucleoli of each haploid set are brought together, probably by synapsis of the nucleolar-organizing chromosomes. They fuse at the point of contact and a single large nucleolus is the result (fig. 7). In some of the writer's preparations the fusing nucleoli can be seen attached to two short arms of a bivalent (fig. 7). These probably represent the two nucleolus-organizing chromosomes of the two haploid sets which have undergone synapsis. From this it may be inferred that originally each nucleolus was attached to one chromosome of each haploid set, which confirms Olive's observations in *Coleosporium vernoniae*. Soon the two nucleoli completely fuse with one another and form a large fusion nucleolus, and after this many chromosomes appear to be attached to it (fig. 11). Occasionally the nucleoli do not fuse. In such a case a nucleolus becomes detached from its organizers and becomes smaller and smaller (fig. 12) until it is finally lost. This occurs very rarely, however, and may be considered as an exception rather than the rule.

The next stage is different from that met with in higher plants. In higher organisms the pachytene threads become thicker and shorter but in *Coleosporium*, as has already been remarked by Olive (1949), the chromosomes instead of shortening become very long and narrow (figs. 15 and 16). Following Olive, therefore, the writer prefers to call it the "phase of elongation" of the chromosomes. It is normally impossible to see the four-strand stage and whether the bivalents split up is a matter for speculation. However, they never form a reticulum. In later stages of the "phase of elongation" the chromosomes are very narrow and long and become arranged in all directions within the much enlarged nucleus (figs. 15 and 16). Another marked feature of the chromosomes at this stage is the conspicuous beading (fig. 15) which can be discerned along the whole length of the chromosomes.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Whether they merely represent the points where the chromatids are wound round one another or whether they are simply thickenings cannot be made out. The appearance, however, is very characteristic and can be used in distinguishing this stage from zygotene.

The behaviour of the nucleolus in zygotene and the "phase of enlongation" is very interesting. In early zygotene the nucleolus comes to lie on one side of the nucleus (figs. 8, 11, 13 and 14). According to Olive (1949) the nucleolus at this stage shows two clear regions. The outer zone takes a dark stain with crystal violet; the inner is less dense and takes a very light stain. The illustrations and description given by Olive imply that there are differences in the density of the nucleolar material at this stage. If the two zones represent the outer denser and inner lighter regions, they should also be seen by the use of other stains. In slides prepared with the crystal violet-iodine techniques such outer and inner zones can be seen in the nucleoli, but such a condition is not characteristic of the nucleoli at the zygotene stage only. Even in early fusion stages the two separate nucleoli can be seen to possess two similar regions (fig. 17). In slides stained with Heidenhain's iron-alum haematoxylin, however, the nuclei in the leptotene and zygotene stages show a uniformly stained structure (fig. 9). During prophase the nucleolus begins to become vacuolated, the vacuoles appearing first in its central portion (fig. 8). With progressive vacuolization, the outer region of the nucleolus collapses and in the pachytene stage it becomes closely adpressed to one side of the nucleus (fig. 13b) where it is seen as a flat disc-shaped, darkly staining structure (fig. 15). It is extremely likely that the nucleolus contributes something to the chromosomes. This suggestion is in keeping with the modern views on the origin and behavior of the nucleolus.

The next recognizable stage is diplotene. The chromosomes contract

FIG. 1. Hyphae ramifying in the intercellular spaces of the host. FIG. 2. A single hyphal cell with two nuclei. FIG. 8. A young probasidial sorus showing the probasidial elements and basal mother cells. FIG. 4. Part of a probasidial sorus showing an emergent probasidium. The shaded portion is the gelatinous matrix. FIG. 5. A single probasidium showing stalk-like base. FIG. 6. Probasidium with nucleus in the fusion stage. The two sets of chromosomes with nucleoli are still apart. FIGS. 7–14. Zygotene. FIG. 7. Two nucleoli fusing to form a single one, each attached to one short arm of a bivalent. FIG. 8. Fusion nucleolus showing two small vacuoles. FIG. 9. Same stage as 8 (Haematoxylin preparation). FIG. 10. Some chromosomes at zygotene stage, showing the double nature of the threads. FIG. 11. Synizesis (Haematoxylin preparation). FIG. 12. Early zygotene, showing a degenerating (small) nucleolus and a normal one. FIG. 13a. Zygotene, with the nucleolus pressed to one side, apparently showing two differentially stained regions. FIG. 13b. A later stage than 13a. FIG. 14. Haematoxylin preparation of the stage corresponding to 13a. FIG. 15. Phase of elongation of the chromosomes. The nucleolus is seen as a dark adpressed band at one side. FIG. 16. Later stage than 15 without any trace of the nucleolus. FIG. 17. Early fusion stage of the nuclei, showing the differentially stained areas in the nucleoli. FIG. 18. Early diplotene, showing the much contracted chromosomes, which reveal a double nature. FIG. 19. Later stage than 18. (All figures × 1150.)

gradually and become thicker (figs. 18–21). The volume of the chromatic material at diplotene gradually decreases. The double nature of the chromosomes can be clearly made out at this stage (fig. 18). Figures suggesting chiasmata are also frequently observed. At diplotene the nucleus becomes smaller and smaller and the chromosomes become more compact (figs. 20 and 21). Diplotene gradually merges into diakinesis and at the end of this stage the nuclear membrane is lost and the chromosomes lie in a compact mass within the nuclear vacuole (fig. 22).

An attempt was made to count the number of chromosomes in late diplotene. The clearest figure indicates that there are eight bivalents. Olive (1942, 1949), in his study of *C. helianthi* and *C. vernoniae*, also gives eight as the haploid number. Holden and Harper (1902) have given eight to ten as the haploid number. Sappin-Trouffy (1896) and Moreau (1914) reported the chromosome number as two.

Metaphase I: The spindle is intranuclear in origin. The beginnings of a spindle can be seen at the diplotene stage with the appearance of delicate strands, which run from the periphery of the nucleus towards the center (figs. 18 and 21). These strands gradually increase in number towards diakinesis (fig. 21), after which they probably arrange themselves into a spindle. The spindle is a only slightly broader in the center and the fibers converge towards the poles (fig. 23). At each spindle pole a darkly staining, minute body can be discerned. The position of this body suggests a centrosome, but its origin is obscure. Olive (1949) states that some darkly staining granules appear at the periphery of the nucleus in early prophase and could be considered as centrosomes. But he was not able to find any trace of them at diakinesis where they should have divided if they were true centrosomes. The writer has noted similar bodies in his preparations.

From the polar ends astral rays are seen to emanate in all directions. These can be recognized in the form of small fibers (figs. 23 and 24). When the spindle has been formed, the chromosomes become attached to it at various places. Normally, in higher plants, the chromosomes are arranged in the equatorial region of the spindle, but the narrowness of the spindle is perhaps the cause of such a behavior in this rust. The chromosomes are disposed separately, although a clumping may appear in some preparations (fig. 25). The spindle of the first metaphase is usually vertical (fig. 23), but sometimes oblique (fig. 24). The writer is convinced that the spindle position is by no means fixed. Generally, if the probasidium is relatively narrow (fig. 23) the spindle will be vertical, but if it is wide (fig. 24) there is enough space for it to be placed even in a horizontal direction.

Anaphase I: In anaphase the spindle fibers tend to coalesce, and in later stages only two strands may be recognized running almost a parallel course (fig. 26). The chromosomes pass to the poles at different rates, so that by

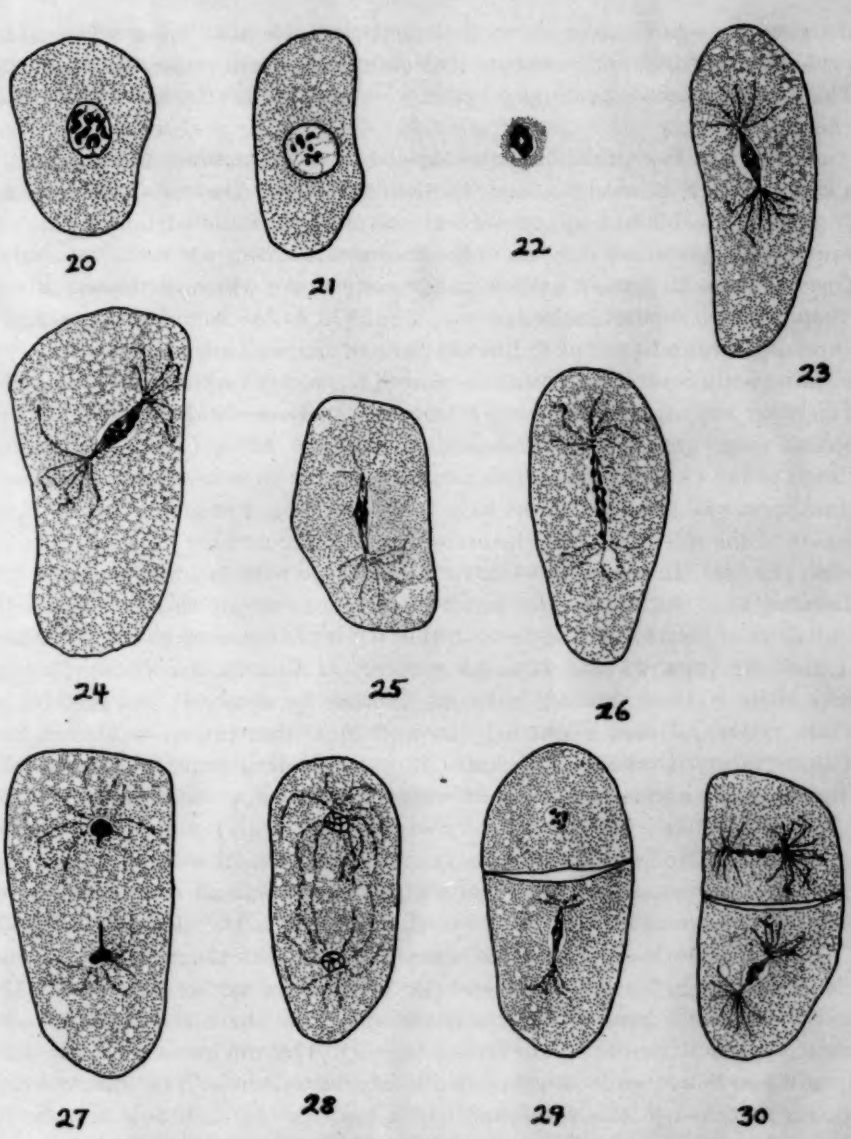

FIG. 20. Late diplotene. FIG. 21. Late diplotene, with the chromosomes very much shortened and thickened. Eight gemini may be counted in the figure. Note the delicate strands running from the periphery of the nucleus to the center. FIG. 22. Diakinesis. FIG. 23. Metaphase I. FIG. 24. Metaphase I with an oblique spindle. FIG. 25. Metaphase I. FIG. 26. Anaphase I. FIG. 27. Telophase. FIG. 28. Interphase nuclei. The astral rays are long and vacuoles are arising in the center of the probasidium. FIG. 29. Second meiotic division. The lower cell is in metaphase, while in the upper one the spindle is about to develop. FIG. 30. Second meiotic division. The upper cell is in anaphase, while the lower one is still in metaphase. (All figures × 1150).

the time some have already reached the poles, others still lag behind. It is probable that disjunction occurs and eight chromosomes pass to each pole. The nuclear vacuole gradually becomes obliterated by the end of anaphase (fig. 26).

Telophase I. At telophase the chromosomes accumulate at each pole in a characteristic bilobed manner. The astral rays are very clear at this stage (fig. 27). The bilobed appearance at this stage led the earlier workers to believe that there are only two chromosomes in *Coleosporium*. The spindle fibers coalesce to form a narrow rod-like structure which ultimately breaks when the two nuclei are organized (fig. 27). A fine nuclear membrane is developed around each of the newly formed nuclei. In some cases a darkly staining body is recognizable at one end of the newly formed nuclei (fig. 28). The polar radiations become very long, curiously curve downwards and intersect near the center of the basidium (fig. 28). Olive (1942, 1949) is inclined to the view that these polar radiations somehow help in cutting out a transverse wall after the nuclei have been organized. Frequently at about the region of the intersection of the astral rays a large number of small vacuoles arise (fig. 28). In some cases the vacuoles marge with one another, and it is probable that the wall is the result of a coalescence of these vacuoles. On both sides of the vacuoles so formed, thin walls are secreted by the cytoplasm of the cell (figs. 29 and 30). As a result of this the basidial cells may have their walls separated from one another by a space. The method by which the astral rays might help in wall formation cannot be determined with certainty. Probably they assist in accumulating some fluid cytoplasm (hyaloplasm) around the vacuole where it secretes a wall. In the case of Ascomycetes like *Phyllactinia corylea* (Harper 1905) and *Gelasinospora tetrasperma* (Dodge 1927) the astral rays function in ascospore delimitation. In these cases they recurve around the nucleus and serve to gather a bit of cytoplasm around it, after which a cell wall is laid down on all sides.

Second meiotic division. This is much briefer than the previous division. The nuclei formed after first telophase do not have any resting phase. The first recognizable stage is the condensation of the chromatin material into small, compact, rod-like structures (fig. 29). The nuclear membrane soon dissolves and a spindle appears in the nuclear vacuole. The chromosomes become attached to this spindle at various points. At each pole may be recognized a darkly staining body, which again represents either a centrosome or the point of convergence of the fibers (figs. 29 and 30). Astral rays are also very conspicuous, as in the first division. Spindles in this division are much shorter than in the first division (fig. 30). Metaphase quickly passes into anaphase and again the spindle fibers become drawn together into two strands (fig. 30). A chromosomal count cannot be made with certainty, because there is a clumping of the chromosomes. The divisions in the

upper and lower cells are not exactly simultaneous. Frequently, when one nucleus is in anaphase, the other is still in metaphase (fig. 30). The spindles are variously oriented (figs. 29 and 30). They may be oblique, longitudinal, or transverse. This is in keeping with the contention of the writer that the position of the spindle is determined by the available space. The spindle being very small here occupies very little space and hence may be oriented in any direction. If the spindle is transverse the wall is laid down vertically and if it is vertical the wall is transverse. Here also the astral rays are very extensive and frequently intersect in the middle although this is not so marked as in the first division (fig. 30). A slight vacuolization of the cytoplasm can be seen in the middle region of the cell as in the first division.

The basidiospore development agrees closely with the description given by Olive (1949) and it is needless to repeat a description of it here. A third division takes place in the basidiospore. Of the two resulting nuclei apparently one degenerates and only one remains.

DISCUSSION

The writer has not been able to discern any trace of catenulation in the basidial sorus of *Coleosporium sidae*. Dietel (1903) and Olive (1949) both reported that some species of this genus regularly show catenulation of their basidial elements. It is possible that within the genus there are species where a catenulation of the basidial elements is not a marked feature, while in others it is. In the microcyclic species; *viz.*, *C. crowellii* and *C. pinicola*, the catenulations are very marked and constitute a very characteristic feature. Thus, a gradation as regards the catenulations can be seen in the genus *Coleosporium*.

There are certain features exhibited in the species under consideration which are believed to be of considerable phylogenetic importance. Olive (1949) and Linder (1940) have already remarked upon these features. In the first instance the fact that the basidium is very variable as regards septation leads one to support the viewpoint that those jelly fungi which show vertical septation in their basidia may have been derived from a *Coleosporium*-like ancestor. The writer has observed in *C. sidae* that the spindle of the first meiotic division in the probasidium may also be oblique and one can easily visualize a condition in which the spindle of the first meoitic division in the probasidium is regularly transverse, in which case the septation will be vertical, and this would indeed be a close approach to the *Tremella* type of basidium where only vertical septation takes place. Furthermore, in many jelly fungi the mode of septation is not regularly fixed. It may vary from an oblique septum to a regularly vertical one. Many authors have shown that in some species of *Tremella* the septations are not always longitudinal but they may also be oblique. Olive (1949) remarks in his paper that

there are some species of *Coleosporium* in which septation of the basidium is fixed in character. Thus between *Coleosporium* and *Tremella* there can be traced regular gradations of basidia which vary as regards their mode of septation. On the one hand we have those species of *Coleosporium* which show a linear tetrad in the basidium and on the other hand those species of *Tremella* where the basidium is vertically septate. Between these two extremes are the species, both in *Coleosporium* and *Tremella,* which show various intergrading conditions. In the second place, the presence of a gelatinous cover over the probasidial elements in the Coleosporiaceae and Tremellaceae may indicate a further relationship between them.

A relationship of *Coleosporium* with some Ascomycetes might also be considered. The presence of the astral rays is a case in point. The presence and function of such astral rays has been amply demonstrated by Dodge (1927), Harper (1905) and others in members of the Ascomycetes. The astral rays in those cases recurve around the nucleus and serve to delimit a unit of cytoplasm around each nucleus. According to the viewpoint of Olive (1949) and in the opinion of the writer the astral rays in *Coleosporium* are also believed to function in delimiting the basidial septa, assisted by the coalescence of vacuoles in the central region. Probably the third division in the basidiospore is also a point in support of the Ascomycete ancestry of rusts.

It might also be desirable to examine the concept of Savile (1939) about the so-called "expanded" and "unexpanded" type of nucleus in the rusts. A study of the nuclei in *Coleosporium* has convinced the writer that there is little advantage in retaining this terminology, at least in *Coleosporium.* The "expanded" type of nucleus, according to Savile, is present in the urediospore, teliospore and aeciospore while the "unexpanded" type is present in all those cases where the nucleus has to migrate through a narrow pore. According to the ideas of Savile the nucleolus can often be seen as a small granule inside the so-called nucleolus which he calls "endosphere." Olive (1949) has very ably shown that the nucleolus in *Coleosporium* is probably an equal homologue of the nucleolus in higher plants, considering that other features in the cytology of the rust are similar to those met with in higher plants. Thus a nucleolus organizer and "chromatid bridges," very similar to those described by McClintock (1938) in a study of meiotic phenomenon in the microsporocyte of corn, have been demonstrated. There are sufficient features in the cytology of *Coleosporium* to show that perhaps the phenomenon involved here is, after all, not so different from that in the higher plants, and is definitely not "a far cry from the nuclei of the higher plants" (Allen 1933).

SUMMARY

1. A study of the morphology, karyogamy and meiosis in the rust *Coleosporium sidae* has been made.

2. There is no catenulation in the formation of the basidial elements. A gelatinous covering is secreted by the probasidia on the outside and toward the sides. The probasidium is formed from a binucleate basidial mother cell following a conjugate division of the nuclei. The two nuclei slightly enlarge in the probasidium and fuse. The prefusion stage is considered similar to leptotene.

3. In zygotene a pairing of the chromosomes takes place and the nucleoli fuse with one another. There are probably nucleolus organizers in this rust. Generally a fusion of the nucleoli takes place in zygotene, but sometimes a nucleolus may degenerate. Towards late zygotene, there is a tendency of the chromosomes to collapse to one side and this is considered to be a synizetic phase. The nucleolus is pressed to one side and becomes vacuolated, the outer rind collapsing into a discoid structure which stains very darkly.

4. At the "phase of elongation" the four-strand stage cannot be recognized, but the chromosomes appear beaded. Instead of contracting, the chromosomes elongate and become slender. The nucleolus is ultimately lost during this stage.

5. In diplotene and diakinesis the chromosomes contract very much. About eight bivalents may be counted at this stage, and eight is believed to represent the haploid number in this rust. The nuclear membrane is lost at this stage and the chromosomes lie in the nuclear vacuole. The spindle is intra-nuclear and the chromosomes become attached to it at various places. The spindle axis may be longitudinal or oblique. The presence of a centrosome is left open to question.

6. The anaphase is brief, at which time the paired chromosomes are believed to disjoin and eight pass to each pole. Astral rays are very long at this stage and sometimes intersect at the middle of the basidium.

7. The cell wall probably arises by a lateral coalescence of vacuoles.

8. There is no resting phase between the first and second meiotic divisions. The spindle of the second division may be oriented in any conceivable manner, and depending upon this orientation the septa are variously arranged. Metaphase and anaphase are similar to the first division except that the spindle is much shorter.

9. One further division takes place in the basidiospore.

10. The possible relationship of this rust with the jelly fungi on the one hand and the Ascomycetes on the other has been discussed .

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A HEAT CHAMBER FOR THE STUDY OF THE CROWN GALL DISEASE UNDER CONTROLLED TEMPERATURE AND HUMIDITY[1]

MICHAEL LEVINE[2]

Various physical and chemical agents have been applied to overgrowths produced by the inoculation of plants with the bacterium, *Agrobacterium tumefaciens*. The application of heat and humidity on the incipient developmental stages of these tumors has yielded results of considerable interest. Two phases of these thermal studies have now clearly developed. In the first instance, inoculated plants (tomato, *Sedum, Bryophyllum*) kept at temperatures up to 31° C. produced galls but failed to do so when maintained at higher temperatures. However, *Nicotiana glutinosa, N. tabacum* and a tobacco hybrid grown in chambers with temperatures above the critical one also developed crown galls (Riker 1926 and Riker, Lyneis and Locke, 1941).

In the latter report (Riker, Lyneis and Locke, 1941), one finds that the indicated heat was produced by six 500 watt lamps which were cooled by running water. Reference is made to the control of the temperature although the relative humidity is given as 70 per cent. Riker concluded that temperature is correlated with the physiological activity involved in pathogenicity. The pathogenicity seems correlated more with the host than with the bacteria.

Braun (1947), in his studies on the factors responsible for tumor development, localized inoculated areas on the periwinkle stem and subjected them to heat treatment for periods of five weeks. These parts of the plant were introduced into a glass cyclinder through which cool air was blown to maintain temperatures at 26° C. Another device consisted of a wooden pillbox-like chamber thermostatically controlled. A number of holes on the sides permitted the box to enclose five-inch lengths of the inoculated stems of a potted plant. The heat-treated areas, kept at 32° C., produced no tumors. The inoculated parts of the plant protruding above the box produced overgrowths. Braun concluded that environmental conditions that exist in the immediate surroundings of the inoculated areas are responsible for the

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Assisted by E. G. Bennett, Jr. to whom the writer is indebted for the construction of this chamber.

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Green house facilities were made available at the Bedford Hills Sanatorium.

[2] Dr. Levine died on August 26, 1952, at the age of 66.

inability of the bacteria to bring about changes of normal cells to tumor cells. These changes were not the result of physiological disturbances in the plant as a whole.

Braun's (1943) earlier work on the effect of heat on tumor inception represents the second phase of these thermal studies. These experiments on the periwinkle, exposed to high temperature and high relative humidity for three to five days after the incipient tumors have developed for two to four days, produced "potentially autonomous bacteria-free malignant growths." Braun used a thermostatically-controlled chamber in which the relative humidity was considered although apparently not controlled.

Theis, Riker and Allen (1950) repeated these thermal studies made by Braun. They built a chamber in which an inoculated periwinkle could be subjected to high temperature (46°–47° C.) and high humidity (80–85 per cent) to destroy the crown gall bacteria. This chamber was made of pine wood, measured five feet in the three dimensions, with a double top and bottom separated by a layer of peat moss. Heat was furnished by an overhead thermo-strip and controlled by a mercury thermostat. The humidity was supplied by a 250 watt frosted bulb wrapped in absorbent cotton, placed in a pan of distilled water. The relative humidity was determined by a psychrometer equipped with an electric blower. A six-inch electric fan distributed the heat. Glass cylinders were also used to encase localized regions of inoculated parts of the periwinkle stems.

In these studies a more determined attempt was made to study the effects of continuously uniform high temperatures and high humidity on inoculated periwinkles. While the heating element of the humidifier (electric bulb) was controlled, the water was supplied manually.

Henderson and Hunt (1951) constructed a non-heating spray-atomizer-humidifying device in an Avena assay room in which a constantly controlled humidity, ranging from 80 to 90 per cent, was maintained. The desired temperature in this room was 24°–26° C. and required no controls since the incoming air was controlled by a thermostat. The problem presents difficulties when both temperature and humidity are high, and both heat and water vapor are produced within the experimental chamber.

In attempting to secure cytological material of periwinkle stems inoculated with *A. tumefaciens* subjected to high temperature and high humidity, several devices were employed. Glass cylinders were used and drying ovens were converted for the purpose. In none was the temperature uniformly constant, especially when the cylinders were used, and in no instance was the humidity accurately controlled for continuous periods of time.

The purpose of this report is to describe a small heat chamber which has been evolved in the course of this study. This chamber has been maintained at constant and continuous high temperature for several days. The

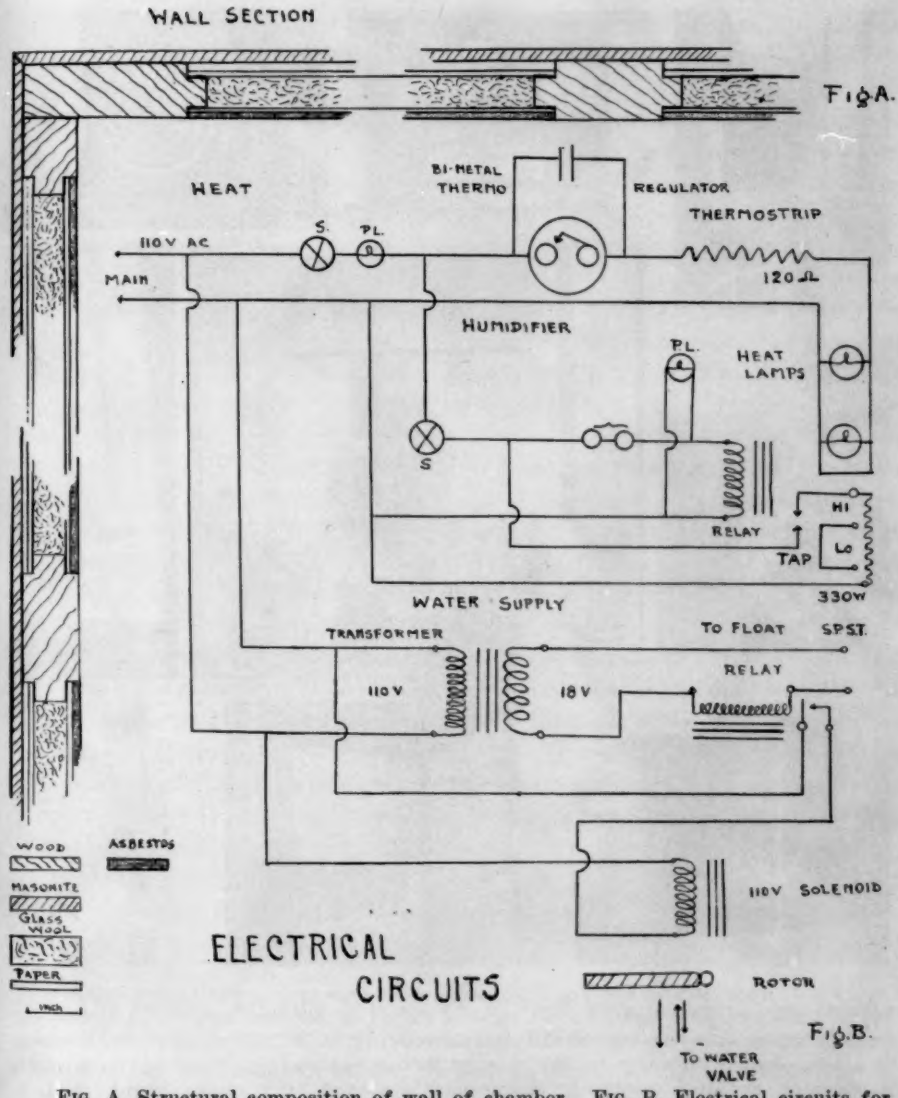

FIG. A. Structural composition of wall of chamber. FIG. B. Electrical circuits for the production of heat, humidity and water supply for humidifying purposes.

relative humidity has been controlled within certain ranges and periods well within the needs of the experiment. This chamber served, first, for maintaining temperatures of 28°–37° C. with 50 to 60 per cent relative humidity, on a variety of garden plants inoculated with *A. tumefaciens*. Temperatures at 45°–47° C. with relative humidity ranging from 50 to 60 per cent and from 80 to 85 per cent were tested on the periwinkle. The proposed cytologi-

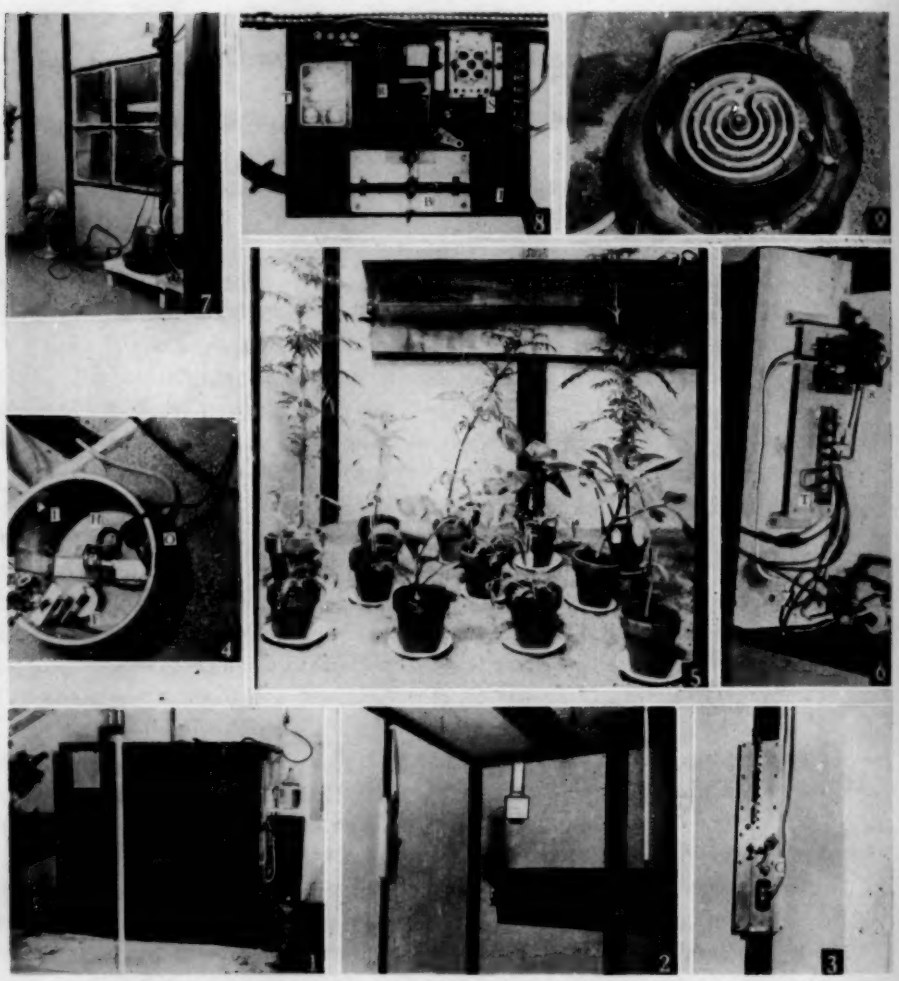

FIG. 1. Heat chamber showing 3-paneled, double-glass door, a small panel with electrical switches and pilot light. To the right, a supply of distilled water with siphon for humidification, emptying into aluminum reservior (figs. 4 & 7). On top of the chamber is a dome-shape glass cover for the bi-metal thermo-regulator; in front and to the left, a standard, approved centigrade thermometer protected by a copper guard. FIG. 2. Interior of chamber, showing pine frame work with interior coating of asbestos; thermostrip, hygrometer, themometer and humidity control device; tip portion of bi-metal thermo-regulator. FIG. 3. A detail of the humidity control device; the contact at "C" is controlled by expansion and contraction of catgut, as affected by humidity. FIG. 4. Electrically-controlled humidifying apparatus. (I) water inlet, supply of distilled water siphoned from container outside of the chamber. (H) immersion heater; (F) float, level of which activates solenoid (S). Water drip from the inlet is taken off at a certain level by the overflow tube (O). FIG. 5. View of interior of chamber, showing distribution of plants to be heat treated. FIG. 6. Small panel with tap (T) and relay (R) in circuit with humidifier control shown in fig. 3. FIG. 7. West corner of chamber, 4-paneled double

cal studies are in progress and it seemed of biological interest to report on the structure and electrical controls of the chamber that made the study possible.

The chamber. The chamber was built in the greenhouse and takes the form of a five-foot cube. In its development, a frame of seasoned, clear pine was built with rabbet joints. The uprights measured 3″ × 1⅛″ and were rabbeted. The south and east spaces were divided by pine strips of the same dimensions, while the west wall was divided by two uprights extending the height of the chamber, to form the supports for a four-panel, double window, measuring 2′ × 2′. The north space of the frame work was provided with two pine uprights of similar dimensions to form the frame work for a 4′ door made and provided with three double panels of glass 17″ wide × 13½″ high. The door was fitted with gaskets and secured by two "dog" catches. The roof of the frame was divided into two panels by strips of pine of the same dimensions. The frame work rested on a cement floor. The floor space was divided into three equal parts by strips of pine and fashioned to hold uniformly cut slabs of cork 3″ thick. This was covered by a 1″ layer of washed sand. The double rabbeted edges of the pine strips served as attachments for the asbestos, paper, glass wool and masonite of which the walls were made. Sheets of brown paper were nailed to the frame work on the inner grooves of the uprights and this was covered with asbestos 3/16″ in thickness, thus forming the interior wall of the chamber and exposing the pine strips so that various instruments could be attached to them. A layer of glass wool was stapled to the paper and wood of the frame from the outside of the chamber. This, in turn, was covered with another layer of paper attached to the outer groove of the frame. The whole was then covered with masonite ¼″ thick. The roof was treated like the vertical wall. The structural make up of the chamber is schematically represented in figure A. The outer walls and ceiling of the chamber were painted in brown paint and finally covered with a thick coating of aluminum paint. The completed chamber is shown in figure 1, before the aluminum painting.

The heating system. Two sources of heat were primarily employed in this chamber. A thermo-strip measuring 42″ long was placed on the mid rear wall of the chamber, backed by a sheet of copper for reflection (fig. 2). Two clinical vascular lamps were put in the same circuit as shown in figure B. These served two purposes: they indicated when the heating

windows and small humidifying system used in conjunction with temperatures below 37° C. and the production of low controlled relative humidity 40 to 60 per cent. A ten-inch fan for distribution of heat and water vapor; a lamp (L) in the circuit indicates the operation of the immersion heater. FIG. 8. Small panel with transformer (T), rotor (R), and solenoid (S). (B) represents a small metal bar held in place by a small spring which presses against a small, thin rubber tube connecting the water supply and the water inlet tube to the humidifier. FIG. 9. A small electric stove in conjunction with the low humidity requirements shown in figure 7.

system was in operation and augmented the heat of the thermo-strip. The lamps, individually, thermostatically controlled, were regulated and controlled, as well as the thermo-strip, by a bi-metal thermo-regulator (fig. B). The regulating element was housed on the roof of the chamber with the sensitive elements projecting into chamber, the tip of which is seen in figure 2. A standard tested thermometer projected into upper part of the chamber through the ceiling, while other thermometers were suspended in the chamber at different levels. The intensity of the heat was varied for low and high temperature by the use of a tap in the circuit, illustrated in figure 6. A small fan was employed to keep the air in circulation. Heat was also produced by the humidifying system and the operation of the fan.

The humidifying system. Two types of humidifiers were employed in this work. For low-range temperatures and humidities, a small electric stove (figs. 7 and 9) furnished the heat for vapor production. Distilled water was siphoned to an aluminum reservoir through glass and rubber tubing from a flask supported on a rack attached to the outside wall of the chamber. The water flow was regulated by the level of a float in the reservior (fig. 7). An overflow outlet which passed from the reservior through the wall of the chamber was provided. Normal relative humidity up to 65 per cent was maintained for a number of days without opening the chamber.

For higher humidity ranging from 70 to 85 per cent, water vapor was produced by an immersion heater shown in figures 3 and 4. This heater was placed in the electrical circuit with a humidifying control device shown in figure 3 and a necessary relay (fig. 6). The light from a small electric bulb, shown in the upper-right-hand corner of figure 7 indicated the operation of the immersion heater. The humidifying control element consisted of a length of surgical catgut "00". With its expansion and contraction, the circuit was made and broken. When the gap measured 0.002 inch, the circuit was closed, the small lamp was lit, the immersion heater was in operation and vapor was produced. The measurement of the gap had to be adjusted in experimental trials before plants were set in the heat chamber. Once in operation and the desired humidity attained, it operated efficiently, although the lag in response measured up to seven minutes.

The water supply. The supply of water for the humidifier is controlled by a float shown in figure 4. As the water reaches a certain level, the float activates a solenoid (S, fig. 4). This sends a current into the transformer (T, fig. 8) which operates a rotor. The distilled water, when siphoned from its container, runs to inlet I shown in figure 4. In its course, a bar attached to the rotor shuts off the flow of water or releases it as determined by the level of the float. The bar of the rotor presses against a thin rubber tube, part of the siphon (fig. 8). This tube is of thin resistant rubber as in the ink sac of a fountain pen. The spring which holds the bar against

this delicate tube may loosen and cause water to drip into the reservoir. An outlet for an overflow is provided to prevent injury to the immersion heater.

Humidity was measured by a self-registering mechanism consisting primarily of hair, shown in figure 2, and a psychrometer. The air movement over the wet bulb was provided by a fan. The psychrometer was placed at the height of the plants treated and so that it could be observed through the window, which was coated with glycerine. In the experiments conducted, the humidity was recorded every quarter hour through the day and at longer intervals through the night.

Figure 5 shows a series of plants in the chamber at temperatures 36°–37° C. A dozen garden plants commonly used in the study of the crown gall disease may be conveniently placed in this chamber. With periwinkles, only one mature woody plant can be exposed at a time. The determining factors in freeing incipient crown galls on mature periwinkle plants of their inciting bacteria seems to be the constant application of high temperature and high relative humidity. This plant may carry as many as 150 to 300 points of inoculations. Exposure of the periwinkle to high temperature, 46.5° C., and high relative humidity, 80 to 85 per cent, for 24 hours caused the growing points and many apical leaves to brown and die. The surviving plants, after these heat treatments, form new leaves and develop tumors slowly. Longer exposures (40 hours) under these conditions have caused death of the entire plant. Treatments carried out at these high temperatures coupled with a relative humidity ranging from 50 to 65 per cent for 72 hours produce browning of leaves together with death of the growing points; the axilliary buds, however, form new leaves within a week to ten days and the inoculated areas of the stem in the more mature parts of the plant show the beginning of crown galls. *Vinca rosea* is moderately sensitive to *Agrobacterium tumefaciens* as pointed out by Braun. The tumors formed in a given period are small as compared to those on the tomato, Bryophyllum, marigold and tobacco.

SUMMARY

1. A heat chamber is described for the purposes of testing the effect of high temperatures and high relative humidity on plant overgrowths.

2. This chamber is provided with an automatic, electrically controlled device for heating, vaporizing water and feeding water for humidification.

3. Preliminary trials have furnished material for cytological study of the effect of heat and humidity on plant tumor development.

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TORREYA

BOOK REVIEWS

New Britton and Brown Illustrated Flora of the Northeastern States and Adjacent Canada. By Henry A. Gleason. 1727 + lxxxii pages, about 4650 species illustrated. New York Botanical Garden, New York 58, New York. December 10, 1952. Price $30.00 plus 50¢ postage, (or $27.50 postpaid before July 1, 1953.)

The two former editions of "Britton and Brown" have been widely used by professional botanists and amateurs alike, the feature of having an illustration supplement the description of every species proving especially helpful. To be sure, some of the drawings were not as accurate as could be desired (at times even contradicting text-descriptions) and led to occasional misidentification, but on the whole they served their purpose. Difficulty arose, too, from the taxonomic-nomenclatorial procedures followed: Dr. Britton was inclined to split families, genera, and species on trivial or elusive grounds; and he followed an American Code of Nomenclature—indeed, his own individual interpretation of certain rulings of that code. As a result, non-specialists often found difficulty in correlating the taxa with those in standard works with less subdivision and with International Code nomenclature.

In 1939 the Board of Managers of the New York Botanical Garden authorized the preparation of a third edition. Dr. Henry A. Gleason, Head Curator there, spent over ten years on this project, and was able before his retirement to bring it to completion. This has now been published in a format similar to the familiar one of the previous editions, although the illustrations are now grouped instead of being inserted individually. Though superior to those formerly furnished, they again do not always agree well with the text.

Volume 1, of lxxv plus 482, total 557 pages, comprises introductory material, and the treatments of Pteridophytes, Gymnosperms, and Monocotyledons. A Preface, by Director Robbins, outlines the history of the project and makes acknowledgment to specialists who aided in various phases of the work. The Introduction, covering 29 pages, is well adapted to encourage and inform the "interested laity," for whom Dr. Robbins indicates the work was primarily prepared. It comprises 22 brief chapters, covering such topics as the history of the vegetation of the region covered, the development of knowledge of the flora, the spelling, pronunciation and application of technical names, rules of nomenclature, classification into categories, how plants are studied and preserved, and the use of keys. A 20-page general key to the major plant groups and families follows. This and subsequent keys are arranged on the inset-line plan, and are dichotomous or at a few points terminally trichotomous. They are often hard to follow from diagnosis to conclusion because there are no leaders across mid-page, but appear to be technically adequate. An unusually full list of botanical authors and a nine-page glossary are conveniently placed in advance of the text proper.

The plant families are taken up in the widely used Engler-Prantl sequence, although Dr. Gleason points out (p. xxvii) that this scheme contains serious errors; he considers it expedient to retain it because of lack of unanimity among botanists as to alternative plans. For each family there is given a key to genera, and for each genus (unless monotypic) a key to species. The binomials are in bold face type throughout, without indication by any deviation as to which taxa are introduced. Species epithets are capitalized when derived from names of persons or from former single names. In cases of subdivision into infraspecific categories, the modern plan of repeating the species epithet for the group including the type is followed. In most cases variety is the favored category, but in certain families subspecies are admitted.

Plant ranges are consistently stated first from northeast to northwest, then southeast to southwest limiting states. They are not as complete as could be desired, giving the

impression of having been based too largely only on specimens which had chanced to reach the Britton Herbarium. Remarks as to status of a few adventives are not especially realistic; to suggest that the grass *Eulalia vimínea* (v. 1, p. 240) is "possibly not established" does not appeal to the southern Pennsylvania botanist who sees floods of it overwhelming the native herbaceous vegetation in our creek valleys. We will agree that *Hieracium sabaudum* (v. 3, p. 527) is indeed a weed elsewhere than in Massachusetts, without needing the qualifying "probably." Common names are added when they really exist, but the practice followed in the previous editions of coining such names for all the taxa is well discontinued. The pronunciation of technical words, and the derivation of species epithets, are not indicated.

The current International Code of Botanical Nomenclature is followed, so that most names correspond to those in general use in this country and abroad. At the close of many species descriptions alternative names are inserted, notably those used in "Gray" (Manual, ed. 7, 1908), "B. & B." (Illustrated Flora, ed. 2, 1913), "Small" (Manual Southeastern Flora, 1935) and "Rydberg" (Flora Prairies and Plains, 1931). The manuscript was completed before the appearance of the 8th edition of Gray's Manual, so that no direct reference could be made to the usage in it, although certain of Fernald's previously published views as to nomenclatorial problems are noted. In spite of the same code being followed, there are so many differences in the names used for the taxa in these two comprehensive works on the flora of essentially the same area, that a convenient-sized check-list with the respective names in parallel columns would be exceedingly useful to every student of the plants.

The text for Pteridophytes was contributed by C. V. Morton, and both it and the accompanying drawings are excellent. It starts with the now admittedly primitive Club-moss Family, and ends with the specialized shield ferns. Except for a cumbersome grouping of the spiny woodferns, this treatment is the best that has yet appeared for this Plant Division. The Gymnosperms are taken up under 4 families, Taxaceae, Pinaceae, Taxodiaceae, and Cupressaceae.

The early groups of Monocots are well described and illustrated, although a few omissions may be noted, as *Typha glauca* in the Cat-tail Family, and *Alisma triviale* and *Sagittaria weatherbiana* in that of Water-plantains. For the Water-weeds *Anacharis* is preferred to *Elodea* or *Philotria*. The treatment of the grasses follows in general that of Hitchcock, and the manuscript of them was reviewed by Mrs. Chase. *Carex* is divided into 57 species-groups, with 220 species (as against Fernald's 267) recognized. The fine illustrations made for Mackenzie by H. C. Creutzberg are used.

In the Arum Family the name *Arisaema triphyllum* is retained in its usual sense, with three varieties recognized, *triphyllum*, *pusillum* and *stewardsonii*. By oversight the key-lines ascribe basal fluting of the spathe to all, instead of only the last. The Lily Family is treated in the comprehensive sense, and *Allium* and related genera are retained in it instead of being shifted to the Amaryllidaceae as done by some enthusiasts. The notable American Lily-of-the-Valley, *Convallaria montana* is not mentioned.

In the Orchid Family, the genus *Habenaria* is not split as was done in the earlier editions. The American Yellow Lady-slippers are considered identical with the European *Cypripedium calceolus*. For the Rattlesnake-plantains *Goodyera* is used; in the illustration, the epithet *ophioides* got misplaced under *G. pubescens* instead of *repens*.

Volume 2 of iv plus 655 pages covers the Choripetalous Dicots from Lizards-tail to Gums. The treatment of the Willows, by C. R. Ball, is very well worked out, and the illustrations of this genus especially good. Regrettably it is not possible to say the same about the Oaks. The drawings of the acorns, which many students will turn to first, seem to have been based on aberrant individuals or hybrids in many cases, notably *Q. bicolor* and *Q. macrocarpa* (p. 42), *Q. ilicifolia* and *Q. marilandica* (p. 45), *Q. velutina* (p. 46), and *Q. coccinea* (p. 47). The paucity of synonyms will cause difficulty here too; the Basket Oak is named *Q. michauxii* without any indication that for many years this has been included in manuals and tree-books (even though erroneously) as *Q. prinus*. Similarly the Chestnut Oak is named *Q. prinus*, and the widely used synonym *Q. montana* is not

given. The Red Oak is classed as *Q. borealis*, but in this case synonymy and discussion are added. The very distinct Yellow Oak (*Q. muhlenbergii*) is reduced to varietal status under *Q. prinoides*.

Usage as to genus segregation differs from that of the current Gray's Manual in some families. Thus, *Hexastylis* is accepted as distinct from *Asarum*, *Tovara* is kept under *Polygonum*, *Oxybaphus* and *Vaccaria* are considered independent genera. For the White Baneberry the species epithet *alba* is retained, *brachypoda* used by Rydberg being given as a synonym, but *pachypoda* of Gray's Manual left out.

Coming to the Rose Family, the treatment of *Rubus* has much to commend it. Only 24 species are admitted, and half of these, constituting the Blackberries, are treated as Collective Species, with numerous geographic races currently classed by enthusiasts as quasi-species listed under the appropriate major taxa. On the other hand, the simple keys and species descriptions given for *Rosa* will scarcely serve to interpret the material one frequently encounters. *Aronia* and *Sorbus* are segregated as genera, while *Malus* is not. *Crataegus* was contributed by E. J. Palmer, 102 species being recognized, and both text and illustrations are excellent.

The broad group Leguminosae is well separated into the 3 families *Mimosaceae*, *Caesalpiniaceae*, and *Fabaceae*. The illustrations in the last are not all as lifelike as might be desired; that of *Cytisus scoparius* (misspelled with a final *a*) on p. 397 does not show enough foliage to aid the beginner. *Astragalus* is kept together, 18 native species being recognized. On the plate p. 423 *Scorpiurus* is accidentally abbreviated to *O.* Most of the 22 species of *Desmodium* are illustrated by but a solitary leaf and fruit, and one would have welcomed a view of the contrasted plant habit of such pairs as *D. "mudiflorum"* and *D. glutinosum* (which incidentally is scarcely as glutinous as shown).

American Woodsorrel, widely known as *Oxalis montana*, is put back into the European *O. Acetosella;* its beauty is not brought out by the figure. The current dispute as to the naming of a couple of weedy spurges is decided (though not settled) by naming the tall, large-leaved taxon *Euphorbia preslii*, and the prostrate, small-leaved one *E. maculata*, the widely used epithet *supina* not being mentioned. *Viola odorata* got lost from its figure on p. 560.

Volume 3, of iii plus 546 text and 44 index, total 593 pages, covers the Sympetalous Dicots, from Sweet Pepperbush to Goats-beard. As in the other volumes, the text and illustrations vary in quality from one group to another, and diagnostic features (as well as spelling of epithets) have sometimes been missed by the artists. Thus, on the very first page, the key attributes to *Clethra acuminata* hirsute filaments, the figure shows them glabrous; on page 4 the calyx of *Pterospora* is described as glandular, but the hairs are drawn as pointed. The Rhododendrons on page 10 were manifestly not drawn from living specimens. *Eubotrys* is maintained as a genus separate from *Leucothoe*, but on the other hand *Chiogenes* is appropriately merged with *Gaultheria*. The treatment of the blueberry series under *Vaccinium* (largely based on the studies of W. H. Camp, as acknowledged in the preface) is especially realistic, the polyploid taxa being clearly indicated, and classed as species; the diploid high-bush taxon which has contributed so much to the large-fruited commercial blueberries is distinguished, as *V. australe*, from the *V. corymbosum* complex. The drawings of the cranberry group are, however, disappointing.

On page 37 there is a slip under *Dodecatheon amethystinum:* it actually blooms two weeks *earlier* than *D. meadia*. The genera *Steironema* and *Naumburgia* are well kept distinct from *Lysimachia*. The detailed views of the Gentian flowers, on which identification largely depends, are regrettably poor; that of *G. andrewsii* is wholly erroneous, that taxon having as stated in the text very short lobes. The corollas of the taxa on page 67 likewise do not agree well with the text descriptions. In the Milkweed Family, *Acerates* is well maintained as an independent genus. The artist had difficulty in proportioning corolla-tube and limb in the Morning-glories, and spelled one *Cuscuta* epithet wrong on p. 95.

The reviewer was pleased with the general high quality of the *Phlox* illustrations,

noting only that the artist had failed to appreciate the chalice involucre of *P. amoena*. To say that *Verbena hastata* has the leaves often hastately lobed may confuse the beginner, since unlobed leaves are those usually met with. The complex Mint family is on the whole well treated. *Scutellaria galericulata* is accepted for American material, and *S. leonardii* maintained as a distinct species. The artist did not note, however, that the text described the petioles of *Synandra* as "often longer than the blades." The genus name *Dracocephalum* is preferred to *Physostegia*. On page 184 the name of *Lycopus virginicus* got lost from its figure; and *Solanum dulcamara* on p. 198 had its initial changed to *P.* Contrary to the antiquated usage of Fernald's edition of Gray's Manual, the genus *Gerardia* is dissected, and *Aureolaria* and *Tomanthera* are awarded generic status. On page 248 a misspelling "artica" was noted. In the genus *Viburnum* the treatment is agreeably conservative, with some poorly differentiated taxa reduced from species to varieties.

The Compositae, treated as a single family, was contributed by A. J. Cronquist. It is divided into ten tribes, which are arranged in a sequence based more closely on evolutionary relationships than the time-honored one. Thus, the primitive Sunflower Tribe, *Heliantheae*, comes first, and is broadened to include the aberrant Ragweed and Cocklebur groups. The Aster Tribe, *Astereae*, now comes fifth, and the rayless tribes seventh to ninth, with only the *Cichorieae* in the usual terminal position. Fairly workable keys, both technical and artificial, are given, and there are instructive enlarged drawings of the diagnostic anther and stigma features.

Noting the usage in certain disputed cases, *Rudbeckia hirta* is accepted in its familiar sense, *Echinacea* being preferred to *Brauneria*, and *Ratibida* to *Lepachys*. Only two species of Cocklebur are admitted, most segregates being lumped under *Xanthium strumosum* L., a trouble-saving but not especially realistic treatment. In both *Solidago* and *Aster* 62 species are recognized. The Horseweeds are segregated from *Erigeron* as the genus *Conyza*. Genus 70, *Antennaria*, receives the least adequate treatment; although there are in the region covered half a dozen taxa of such distinctive blooming period and aspect that they can be recognized from a moving automobile, only 6 species are admitted, most taxa being assigned to varietal status or quasi-synonymy under *A. neglecta* and *A. plantaginifolia*.

In the Chicory Tribe, the first place as most primitive is allotted to *Prenanthes*, with *Hieracium* second. *H. flagellare*, now an abundant weed, seems to have been missed. The creeping Japanese adventive, sometimes called *Lactuca stolonifera*, is well placed in the separate genus *Ixeris*. The final genus, No. 112, is *Tragopogon*, with 3 species, the showiest of all, *T. major*, being listed only as *T. dubius*.

The foregoing remarks will serve to indicate the numerous meritorious features of this worthy successor to the former "Britton & Brown," and at the same time to suggest items capable of improvement. It would help the "interested laity" if the too numerous misprints in the plates, and a few minor ones in the text, were to be enumerated on a correction-sheet, and cared for in a second printing.—EDGAR T. WHERRY, University of Pennsylvania.

Botany. By Carl L. Wilson (line drawings by Hannah T. Croasdale). 483 pp. Illus. The Dryden Press, New York. 1952. $6.10.

Wilson's BOTANY, with its profusion of fine figures, high quality paper, double column format, and large (10″ × 7¼″) bicolor pages, is a striking and attractive new text. The most conspicuous departure from the traditional in text production is the use of red ink, along with black, throughout the book. The red ink is more decorative than functional; broad bands of it outline chapter headings and figures. Leaders, guide lines, and labels are also red. The functional use of red ink does not show much planning or imagination. It might have been used realistically in the printing of chromoplasts, red algae, uredinia, various fruits and other structures that are red in nature. These are printed in black; indeed, a longitudinal section of a strawberry fruit is represented with the achenes in red

and the receptacle in black and white. In the life cycle diagrams, gametophyte and sporophyte structures might have been distinguished by printing one in black and the other in red consistently; in a few of the diagrams the two generations are so distinguished, but in most of them red and black are used with no apparent design.

The 483 pages of text are amply illustrated with 537 figures most of which are beautifully drafted black and whites, by Hannah T. Croasdale, and superlative photographs. These are bled to the margins in the modern manner. Wherever a figure occupies the upper outside corner of a page, the location of page numbers on other pages, the decorative again transcends the functional and the page number is omitted. In deference to figures, for example, there are no numbers on pages between 28 and 40, or between 366–378 and there are many shorter series. The page counting that will be necessitated by references to the many unnumbered pages can hardly be justified on the basis of art in a textbook of science.

The field of botany is well covered and the relative emphasis of the various topics is well balanced. The sequence of topics is one that has found wide favor among teachers of general botany. After the first two chapters, which are designed to orient the student with reference to the science of botany and the nature and use of plants, the author considers the structure and physiology of the vegetative organs of flowering plants. After this, which occupies chapters 3–13, there are two chapters on reproduction in the flowering plants. These are followed by one chapter each on ecology, inheritance, evolution, and classification. The final chapters, 20–30, survey the plant kingdom including the major fossil groups. Students will be aided by the consistent use of boldface type, indicating topics and subtopics throughout the text, and also by the concise summaries that conclude the chapters. The text is terminated by a fifteen page glossary and a fairly complete index, but no references.

The results of recent research are indicated in a number of topics. The treatments of antibiotics and viruses, for example, are up to date and well illustrated. That the oxygen evolved in photosynthesis originates in the water used is indicated; some of the recent work on the application of mineral fertilizers as foliage sprays is mentioned.

The author takes considerable and commendable pains to dispel any teleological views or purpose-oriented interpretations of plant structure and behavior on the part of his readers. This may be typified by the passage, "Adaptations to a dry climate or an aquatic mode of life have not come about because plants have anticipated the need for structural modifications of survival value, nor have the structural modifications arisen in response to a particular environment. Plants have not purposefully adapted themselves to environment, they have survived if their spontaneous mutations and new combinations of genes are fortuitously adapted to their particular conditions of life."

Redundancy of expression may be defended in teaching but it appears to be overdone at some points in the text. For example, on page 17 a symbiotic relationship is described as "Living intimately with another plant (or animal) to the mutual benefit of both" and on page 59 molecules are said to be ". . . in constant motion at all times." Completely indefensible, however, is the implication of causal relationship in a redundant expression, as in the statement on page 424, "Since the ginkgo is dioecious, the pollen and seed strobili are borne on separate trees."

In spite of proofreading and editing, each new textbook of botany has its quota of typographical errors and oversights. This text is no exception, although it has by no means exceeded its quota. Some of the more notable of these are:

p. 23—Fig. 3.1 shows a leaf in the middle of an internode, although internodes are described correctly in the text.

p. 68—*Grana* is used for the singular as well as for the plural; there is more support in Latin for *granum* as the singular, and also precedent for it in botanical literature, cf. E. Heitz.

p. 132—Under the topic *Tissues of the young root.* "In many kinds of plants the cells in the very center of the *stem* mature into xylem. . . ." *Root*, not stem, was undoubtedly intended here.

p. 174—"In nastic movements the direction of the *stimulus* is not related to the direction from which the stimulus comes." This was intended to be ". . . the direction of the *movement* . . ." as it is stated in item 9 of the chapter summary.

p. 205—"If the bee then visits *another flower*, some of the pollen may adhere to the stigma, resulting in cross-pollination." By the author's own definition of cross-pollination, this would have to be *a flower on another plant.*

p. 291—"In *Spirogyra*, the nucleus of the *fertilized egg*. . . ." Earlier *Spirogyra* is described as isogamous and the zygote termed as zygospore.

p. 293—"Gomphronema" should be *Gomphonema.*

p. 389—". . . in order that the sperms may *affect* fertilization. . . ." This, no doubt, was intended to be effect.

Also on this page the figure of the fern archegonium does not conform to the text description.

p. 442—"*Cheledonium*" should be *Chelidonium.*

While, in general, technical terms are used precisely, there are a few instances in which they are violated. The term *tissue* is one of these. Tissue is defined in the glossary as "a group of cells generally similar in origin and function." Yet on p. 73, it is stated that, "During daylight hours, glucose is synthesized in the leaf more rapidly than it moves to other tissues," implying that the leaf is a tissue. On p. 79 we read that, "The leaf tissues are epidermis, mesophyll, and vascular bundles." On p. 132, under *Tissues of the young root* it is stated that, "The third and outermost tissue of the root in a single layer of cells, the epidermis," although the xylem, phloem, parenchyma, pericycle, cortex, and endodermis are described earlier. In the summary of the chapter on roots, too, the stele is referred to as a tissue. In the glossary, however, the terms xylem and phloem are each defined as tissues.

For the most part, the style is lucid and the choice of words suitable for a beginning college textbook, but there are several exceptions that are misleading or at least confusing. On page 56 in referring to a demonstration of osmosis, the movement of water into an osmometer is described as an ". . . inward flow. . . ." The word "flow" connotes a mass movement and can hardly help the student visualize osmosis as a movement of water molecules independent of currents. On page 102 the vascular ray cell which originates in the cambium of a stem is said to be ". . . added to the vascular ray where it elongates somewhat in a *vertical* direction." Since the author is describing structure in a vertical tree trunk, he probably intended this to be *horizontal.* An accompanying figure is oriented as in a vertical stem. Because of horizontal branches and similar complications, it is probably best, in exposition on stem cells, to avoid the terms vertical and horizontal; longitudinal and transverse, or lengthwise and crosswise, are less confusing. On page 261, it is stated that, "Only genes are inherited, not characters." No doubt the meaning intended here is that *genes are inherited, characters are not,* but to state that *only* genes are inherited should perplex the student who is familiar with fertilization, or who has heard of cytoplasmic inheritance. On page 230, we read, "That the forests of Ohio are deciduous rather than *coniferous* is a result of climatic conditions, past and present." *Evergreen* probably was intended here, for the student has at this point not been introduced to conifers. In describing reproduction in *Spirogyra* on page 289, the gametes are described as "nonmotile"; later, the movement of one of the gametes through the conjugation tube is described. An amoeboid gamete is *motile,* even though it has no flagella. On page 323, under virus diseases, infected tulip flowers are described as showing ". . . streaks or lines of contrasting colors in the petals." The accompanying figure shows the symptoms in sepals as well, and the student is apt to conclude that these are petals, even though it is mentioned earlier that the sepals and petals of tulip are alike, and "distinguishable from the petals only by their position." Some teachers of general botany are sensitive about the word *to* and studiously avoid using it where it may be misinterpreted as *in order to.* It is clear that the author does not mean *in order to* for *to,* but there are expressions throughout the text that allow this misinterpretation. For example: zoospores of *Phytophthora* ". . . swim about in rainwater or dew, and finally settle down to form germ tubes which penetrate . . .,"

spores ". . . germinate to produce hyphae," the foot of *Marchantiá* ". . . grows into the tissues of the receptacle to function as an absorbing organ . . .," the "outer spore wall (of pine) enlarges on either side to form a wing . . .," ". . . it (a root or shoot apex) pushes out through the overlying tissues to emerge into the soil or air," and "Bees and other insects visit flowers to gather pollen or nectar as food for themselves or their progeny." The possibility of *in order to* interpretations is easily avoided.

Information presented as factual in the text is accurate and clearly stated except in a few instances where it is misleading or erroneous. In stating (p. 4) that "The first workable electron microscope was built in 1938," the author must have meant "on this continent," for certainly the microscopes of Marton, Ruska and other European workers prior to 1938 must be classified as workable. The statements on page 6 that "The invention of the compound microscope, in 1590, opened vast new fields to the botanist as well as to other scientists. Bacteria and other minute forms of life became visible for the first time . . ." imply that bacteria were first seen with a compound microscope. The view expressed more commonly, that Leeuwenhoek first saw and described bacteria with simple lenses has stronger documentation. The view expressed on page 154 that ". . . these (denitrifying) bacteria are anaerobic, obtaining their energy by the reduction of nitrates and ammonium compounds . . ." should perplex the reader who has just learned that nitrifying bacteria obtained energy from the oxidation of ammonium compounds and nitrites. In considering the origin of vascular plants, the author has espoused the homologous hypothesis; this is understandable, but teachers who follow the antithetic hypothesis will take exception to statements like, "The first land plants, vascular and nonvascular, probably arose from those green algae in which the gametophyte and sporophyte were similar in size.", "The ancestors of the present vascular plants probably arose among the green algae in which the two generations were similar.", and "However, there is wide agreement, as we pointed out in Chapter 20, that the two generations in the life cycle of these ancestral forms were independent of each other and approximately equal in size." To some, the use of "probably" will not compensate for the failure to mention the possibility of an antithetic origin.

In the chapter on classification, the arrangements of plant classes according to the "old" and according to the "new" classification are compared in parallel columns. This is a commendable convenience to students who may have difficulty in correlating readings in "old" and "new" literature. The comparison is followed by a detailed consideration of the major groups in the "new" classification. The "new" classification described differs from the "old" in placing all vascular plants in the Division Tracheophyta, and in the Subdivisions Psilopsida, Lycopsida, Sphenopsida, and Pteropsida. The phylogenetic basis for this arrangement is indicated here, and well supported in the later chapter on fossil plants. While morphologists may take some satisfaction in seeing the classification of major vascular groups in yet another elementary text conform to the preponderant evidence of phylogenetic lines, they will be disappointed in the further classification of the Pteropsida, for here the old Filicineae and Gymnospermae are retained as classes. The retention of the class Gymnospermae, without mentioning that it appears to cut across phyletic lines, seems inconsistent with the arrangement of the larger groups and, as from some other recent texts, beginning students will continue to be led to the view that the Pteridospermae are more closely related to the conifers than they are to the ferns.

The reader should find the glossary convenient, but in some instances he would do better with a dictionary. *Scarification*, for example, is defined as "The seed treatment employed to break dormancy by treatment with acids, abrasives, and by other methods." The student may believe from this that all methods of breaking dormancy of seeds (e.g. stratification and gas treatments) are methods of scarification, whether they involve etching or scratching of the seed coat or not. The definition of a *scion* as "a portion of a shoot used for grafting" will hardly help the student who is confused about which part of a grafted plant to call the scion. *Xylem* is defined as "one of the two component tissues of vascular tissue." *Phloem*, too, is defined as "one of the two component tissues of vascular tissue."

The enumeration of more adverse than favorable criticisms in the above notes may leave the impression that this text is considered inferior to other recent textbooks of general botany. This is in nowise the case. Space does not permit the enumeration of its good points, but certainly it compares favorably with the best available, and it is on the "approved" list for my classes.—EDWARD M. PALMQUIST, University of Missouri, Columbia, Mo.

Drawings of British Plants. By Stella Ross-Craig. Part VI. Portulacaceae, Elatinaceae, Hypericaceae, Malvaceae, Tiliaceae, Linaceae, Geraniaceae, Oxalidaceae, Balsaminaceae, Aquifoliaceae, Celastraceae, Rhamnaceae, Aceraceae. *pl. 1–56*. 10 December 1952. London: G. Bell & Sons, Ltd.

The latest part of this series maintains the high quality of earlier parts (see Bull. Torrey Club **75**: 672; **77**: 406; **79**: 193), and of English iconography in general. The work will be more valuable to the student and teacher of botany than to the collector of plates. The style of the artist is severe, even harsh; but she is skillful in depicting the glabrous "look" of a *Montia* as contrasted with, for instance, *Geranium molle*. The wealth of diagnostic detail should be valuable in identification, even without text. The current part is modestly priced at 10s, about $1.50; since a number of the species are naturalized in this country, it should be a useful addition to an American botanical library.—H. W. RICKETT, The New York Botanical Garden.

Flora of Okinawa, an enumeration of the plants of Okinawa and Sakishima Archipelagos in the Ryukyu Islands. By S. Sonohara, S. Tawada, and T. Amano. 1–231, 1–28, 1–50. (309 pp). *pl. 1*. (mimeographed). 1952.

This is a systematic enumeration of the vascular plants of the southern half of the Ryukyu Archipelago issued by the U. S. Civil Administration of the Ryukyu Islands, under the Department of the Army in cooperation with the indigenous Government of the Ryukyus. It was prepared by Okinawan botanists originally on the request of naturalists in the U. S. armed forces stationed in Okinawa just after the war. It was subsequently augmented and edited by the present reviewer.

The plants of the Ryukyu chain are of interest botanically because they constitute a transitional flora between the temperate and warm temperate flora of Japan and the tropical and subtropical flora of Formosa and South China. The Japanese botanists have only partially studied this area, which before the war was considered by them as the dark area of Japanese botany. With the late war the United States assumed responsibility for these islands and their economic development to a status of greater self sufficiency. The accumulation of scientific knowledge of the area has been a step in this direction. The issuing of this locally prepared Flora is one of the first moves toward a botanical understanding of the economic plants of this area.

This enumeration lists about 2500 species with the original citation, the country whence first described, the name-bringing synonym when needed, the Japanese and Okinawan names as transliterated, the English name when there is one, the distribution in Okinawa-ken (i. e. the Ryukyus from Okinawa Island south), and brief notes on uses. It is not documented by critical examination of extensive herbarium material and the citation of specimens, because such resources were not available to the authors. This flora was issued in mimeographed form, designated as a "preliminary edition," so that it would be available to stimulate and guide Okinawans and westerners who may collect specimens on which a properly documented Flora can be based.

The accumulating of verifying herbarium specimens was considerably advanced in 1951 by the writer's three months collecting trip in these islands. He was there as botanist of the Scientific Investigation of the Ryukyu Islands program being conducted by the Pacific Science Board of the National Academy of Sciences—National Research Council in cooperation with the U. S. Army. (For an account of this expedition see E. H. Walker,

A Botanical Mission to Okinawa and the Southern Ryukyus. Asa Gray Bulletin 1 (3): 225–242, figs. 1–9, July, 1952, published by H. H. Bartlett, University of Michigan.)

A limited number of copies are being distributed by the Publications Department of the U. S. Army in Washington, others by the original authors in Okinawa. Those in this country and in Europe in need of copies should address their requests to the reviewer.—E. H. WALKER, Smithsonian Institution, Washington 25, D. C.

Floristic Relationships Between Eastern Asia and Eastern North America. By Hui-Lin Li. Transaction of the American Philosophical Society Volume 42 (part 2), pp. 371–429 (including 56 maps). 1952. Available as a paper bound separate at $1.00 from the American Philosophical Society, Philadelphia 6.

This is the first comprehensive review and general statement of the problem since the middle of the last century when Asa Gray and F. A. G. Miquel recognized that there were many related genera and species in the floras of eastern Asia and eastern North America. Mr. Li discusses the taxonomy of previously listed taxa exhibiting in their ranges disjunction between Asia and eastern North America. One may not agree with his interpretation that most of the closely related plants are separate species rather than varieties or subspecies of the same species. However, it is clear that they are descendants of the same ancestral population resident in the Tertiary mesophytic forest which probably extended from eastern Asia through Siberia and Alaska to eastern North America.

While only a general statement is made by Li concerning the pertinent Pteridophytes and Gymnosperms, fifty-nine families of the Angiosperms are discussed in detail in regard to related genera and species indigenous to the eastern areas of both continents. He notes that some have related forms in Latin America and suggests a further study of this phytogeographic problem.

No previous discussion of the relationships in the floras of eastern Asia and eastern North America has been so richly supplied with maps. The known distribution of fifty-six genera or related pairs of genera with pertinent disjunct ranges are illustrated in as many maps. Included are: *Saururus, Carya, Buckleya, Pyrularia, Tovara, Hydrastis-Glaucidium, Podophyllum, Jeffersonia, Diphylleia, Caulophyllum, Menispermum, Liriodendron, Magnolia, Illicium, Schisandra, Sassafras, Lindera, Stylophlorum, Penthorum, Decumaria, Astilbe, Itea, Hamamelis, Rhodotypus-Kerria-Neviusia, Gymnocladus, Cladrastis, Wisteria, Apios, Pachysandra, Parthenocissus, Stewartia, Gordonia, Ascyrum, Panax, Nyssa, Tripetaleia-Elliotia, Pieris, Lyonia, Epigaea, Shortia, Halesia, Chionanthus, Gelsemium, Veronicastrum, Campsis, Catalpa, Phryma, Mitchella, Triosteum, Diervilla-Weigela, Zizania, Diarrhena, Croomia, Symphocarpus, Helonias-Heloniopsis,* and *Tipularia.*

That there are occasional minor errors in some maps will come as no surprise to those who have prepared distribution illustrations. Scattered collections and new exsiccati are always severe problems. That the maps for *Carya, Tovara, Hamamelis, Parthenocissus, Nyssa, Gelsemium* and *Mitchella* could have their range outlines depressed further into Latin America detracts in no way from the theme of the paper. The caption under map 50 should read: "*Diervilla* (in America) and *Weigela* (in Asia)." Another error is the statement on p. 381 that *Pyrularia pubera* is a parasite "on roots of *Tsuga*" rather than deciduous shrubs and trees.

The summary includes two lists of genera that are confined to eastern Asia and eastern North America. They are separated on the basis of their distribution: (1) strictly temperate, and (2) temperate and tropical (in at least one continent). Both lists give the growth habit and the number of species in Asia and in America. The bibliography includes 194 items.

For every student of plant distribution, this work is a necessity, and in no other recent phytogeographic publication does one get so much at so reasonable a price.—AARON J. SHARP, The University of Tennessee, Knoxville 16.

BULLETIN OF THE TORREY BOTANICAL CLUB
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